ECOLOGICAL
MONOGRAPHS

CONTENTS

THE VEGETATION OF ISLAND BEACH STATE PARK, NEW JERSEY

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INTRODUCTION

Island Beach State Park (Fig. 1) occupies a 10 mi. stretch of barrier beach or offshore bar located on the New Jersey coast about 50 mi. north of Atlantic City. Lying south of Seaside Park and north of Barnegat Inlet, it is bounded on the east by the Atlantic Ocean and on the west by Barnegat Bay. The average width of the bar is less than 0.5 mi., and the total area of the park is about 2300 acres. Most of these 2300 acres are occupied by a natural cover of maritime vegetation.

According to a resolution of the Torrey Botanical Club (Small 1945), "Island Beach represents a unique example of seashore vegetation, the only undisturbed and well-developed area of this kind of vegetation of any considerable size in New Jersey and the adjacent states." While it is not entirely "undisturbed," the areas within the park in which disturbance has had a notable effect on the vegetation are relatively small, and they can be located and delimited with a fair degree of accuracy. The southern tip of the bar, for example, has been disturbed by the deposition of large amounts of material dredged from the bottom of Barnegat Inlet in 1954. These deposits are easy to identify, however, because they contain many shells and large shell fragments which are not found in natural, windblown deposits. In the early 1930's certain marshy areas were drained by ditches in an attempt to reduce the sizable mosquito population.

The ditches and the mosquitoes are still present. The ditches in large tidal-marshes have produced no apparent change in the vegetation. Those in smaller areas of brackish marsh are now clogged, and pre-ditching drainage patterns have been restored. The only other notable effects of disturbance are confined to small areas around present and former building sites, to narrow strips along the highway down the center of the bar, and along footpaths which lead away from the highway. A few small fires were reported in 1954, and others are said to have occurred during the war years, but there is no convincing evidence for the widespread or frequent occurrence of fire in the past history of the area. By and large the greater portion of the vegetation cover appears to be undisturbed by other than natural causes.

Island Beach became a state park in 1953 when it was purchased by the State of New Jersey from the executors of the estate of the late Henry Phipps. The State's tentative plan for the development and management of this unusual seashore area provides for the maintenance of the northern third as a nature reserve, the central third as a recreation area, and the southern third as a wildlife sanctuary. At the present writing, this plan has not been put into practice nor has the park been fully opened to the public. In planning for multiple-use, park officials hope to preserve and utilize as many as possible of the area's natural attributes. If these goals are obtained, more than two thirds of the area will be maintained in its present near-natural condition. Because it supports
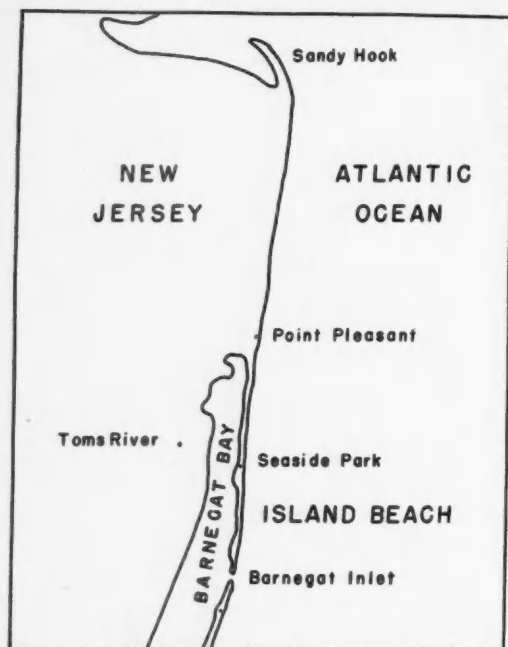
FIG. 1.   Island Beach and Vicinity.

one of the few significant remnants of maritime vegetation in this region, Island Beach is of considerable interest to students of natural history and to proponents of conservation. As a nature reserve in a region where natural areas are rare, it should become increasingly important as an object of scientific investigation in various fields of natural science.

Since Harshberger's study of New Jersey strand flora in 1900 and Chrysler's study of Sandy Hook in 1930, there has been very little ecological work on strand vegetation in New Jersey. Most of the pertinent literature dealing with other maritime areas on the eastern and southern coasts of the United States has been reviewed recently by Oosting (1954). Boyce (1954), Miller & Egler (1950), and Moul & Brown (1957).

The first of several studies reported in this paper was undertaken to provide an inventory of the natural vegetation in Island Beach State Park and thereby establish a basis for future ecological studies of various kinds. Preliminary vegetation maps, based on reconnaissance and ecological surveys, revealed an intricate vegetational pattern made up of numerous structurally and compositionally distinctive plant communities. This complex pattern became the object of speculation and further ecological investigation. Several studies were undertaken to determine the nature of environmental influence on the vegetational pattern; and one autecological study, having to do with the tolerance of plants to windborne salt spray, was completed. The results of these studies provide several kinds of evidence—observational, analytical, and experimental—which have been used in making a fairly comprehensive interpretation of the landscape. In this synthesis of information, Island Beach is portrayed as an extremely diversified but well-integrated vegetation-environment system of great complexity. It is hoped that this approach will add materially to the ecological understanding of Island Beach in particular and to that of maritime strand in general.

AN INVENTORY OF PLANT COMMUNITIES AND VEGETATION PATTERNS

To provide a permanent record of the vegetation of Island Beach State Park in its pre-park-development condition and a descriptive point-of-reference for subsequent ecological study, it was necessary to make an inventory of plant communities, and to describe their character and distribution. The information deemed necessary to complete this inventory includes the following: (1) a fairly complete and ecologically annotated list of the vascular plant species which comprise the flora, (2) a detailed vegetation map showing the distribution of individual plant communities and of man-made features and natural landscape units which support no vegetation cover, and (3) a detailed description of each class of vegetational mapping units.

A fairly complete list of vascular plant species previously reported from Island Beach (Small 1954) was available from the outset. Many additional species and the necessary ecological annotations were supplied by the author. Since this list contains many species which are not vegetationally important, it has been omitted from this report. Plant nomenclature follows Fernald (1950).

METHODS

CONCEPTS AND TERMS

The methods employed in mapping and describing the vegetation of Island Beach are based on the general premise that individual plant communities are the fundamental units of vegetation. For this purpose, an "individual plant community" may be defined as a particular aggregation of plants having uniformity of structure and composition and occupying an area of essentially uniform environment. In the following account of methods and results, groups of communities which are similar in structure and

composition and occupy similar habitats are referred to as "community types." Groups of community types which are similar in structure only are referred to as "vegetation types."

In accordance with the general premise stated above, individual plant communities were employed, wherever possible, as mapping units. Ideally, each "mapping unit class" should represent a distinct "community type," but many recognizable communities are too small to be mapped separately. Consequently, several mapping unit classes (see page 15) actually indicate areas in which two or more community types occur, but the individual plant communities included within the individual mapping units are too small to be mapped separately. A second consideration that makes it necessary to distinguish between "plant community" and "mapping unit" and between their collective counterparts, "community type" and "mapping unit class," is the fact that some mapping units, beach for example, represent areas which are characteristically barren of vegetation.

DESCRIPTIVE CRITERIA

Certain structural, compositional, and environmental criteria based on data and experience derived from preliminary reconnaissance studies were applied as uniformly as possible to the problems of describing, mapping, and classifying the various vegetation components: individual plant communities, community types, and vegetation types.

In locating the boundaries between mapping units and in describing and classifying plant communities, structure or physiognomy was given first consideration. The structural vegetation types recognized on Island Beach (Table 1) are based on the height and relative importance (cover) of the dominant growth-forms.

TABLE 1. Criteria for the recognition, description, and classification of structural vegetation types in Island Beach State Park, New Jersey.

STRUCTURAL TYPES	CHARACTER OF DOMINANT SPECIES			
Name	Growth-Form	Height (ft.)*		Per cent Cover**
Grasslands........	Grasses:	<1 1-4 >4		<20 20- 70 > 70
Marshes..........	Forbs and sedges:	<1 1-4 >4		<20 20 -70 > 70
Herb-Shrub Mixtures......	Herbs: Shrubs:	<1 1-4 >4 <3 3-7 7-15		Highly variable, shrub cover usually <50
Thickets.........	Shrubs and small trees:	<3 3-7 7-15		<50 50-100 >100
Woodlands.......	Tall shrubs and trees:	— — >15		<50 50-100 >100

*Ranges for low, medium, and high.
**Ranges for sparse, open, and dense.

Each community type represented by a different class of mapping units is characterized either by a particular combination of species or by a limited range of combinations. Relative cover was employed as the chief basis for rating species as to their im-

portance in community composition. Abundance, density, and frequency were also used in describing communities and community types while presence, and fidelity were given some consideration in their classification.

In describing habitats, the only factors considered were those which are visually observable and easily estimated. As the major controlling factor (Oosting 1954, Dansereau 1957), topography was given first consideration. Table 2 shows the outline of a tentative classification of topographic conditions. The fundamental units are topographic facets which are described as areas of uniform elevation, configuration, or exposure. Edaphic conditions and exposure to wind, and thus to windborne salt spray, were estimated according to the scales listed in Table 3.

TABLE 2. Tentative classification of topographic conditions in Island Beach State Park, New Jersey*

Topographic Zones	Landforms	Topographic Facets
I. SHORE.................	A. Foreshore	1. Offshore terrace 2. Wave-cut terrace
	B. Backshore	3. Outer beach 4. Inner beach
II. PRIMARY DUNES....... (active)	C. Foredune	5. Seaward slope 6. Top 7. Backslope
	D. Backdune	8. High swale (>5 ft elev)** 9. Low swale (<5 ft elev) 10. Hollow 11. Dunelet
III. SECONDARY DUNES.... (inactive)	E. Foredune	12. Seaward slope 13. Top 14. Backslope
	F. Backdune	15. High flat (>5 ft elev) 16. Low flat (<5 ft elev) 17. Hollow 18. Dunelet
IV. BAYSHORE..............	G. Peaty shore	19. Intertidal flat
	H. Sandy shore	20. Sand ridge 21. Non-tidal flat
AND TRANSVERSE FEATURES	I. Wind channel	22. Blowout
	J. Wave channel	23. Outer 24. Middle 25. Inner
	K. Transverse ridge	26. Outer 27. Middle 28. Inner

*See Fig. 19 for an approximate configuration of the topographic zones.
**More than 5 ft. elevation above mean sea level.

SURVEY AND MAPPING PROCEDURES

Aerial photographs having a scale of 1:10, 560 and permitting stereoscopic examination were used in mapping the vegetation. An outline map showing shorelines, roads, paths, buildings, and other promi-

TABLE 3. Scales for estimating habitat conditions in Island Beach State Park, New Jersey.*

EDAPHIC CONDITIONS		EXPOSURE
Stability and Composition	Moisture and Salinity	To Wind and to Salt Spray
1. Unstable	1. Xeric	1. Extreme
2. **	2.	2.
3. Moderate	3. Mesic	3.
4.	4.	4. Moderate
5. Stable	5. Hydric	5.
6. Sand over peat	6. Brackish	6.
7. Peat over sand	7. Saline	7. Negligible

*The scales are arranged so as to maintain the basic east-west orientation of the principal limiting environmental factor gradients.
**Blank spaces indicate intermediate conditions.

nent landmarks was made by tracing each 9" × 9" photograph separately and then fitting the pieces together.

Using the aerial photographs as guides and the outline map as a key to notes and descriptions prepared in the field, a preliminary survey was conducted to determine the general composition and arrangement of the various vegetation components. In this first survey, the only communities considered were those which could be recognized with certainty and sharply delimited from the surrounding vegetation. Each of these was mapped and described in terms of the structural, compositional, and environmental criteria described above. After the entire area had been surveyed in this manner, it was possible to classify the plant communities so recognized and to set up specific criteria for recognizing the principal vegetation types and community types.

The whole area was then resurveyed, and an attempt was made to determine the status of those areas whose vegetation cover or environment or both are transitional or complex or of an otherwise indeterminate or variable nature. With these additional data, it was possible to devise a tentative scheme for the recognition and classification of mapping units.

The third and final survey was made for the purpose of mapping the entire area and indicating the vegetational composition of each sub-area or mapping unit. The same structural, compositional, and environmental criteria used to recognize, describe, and classify the various units of composition (plant communities and community types) were used again to recognize, describe and classify the various units of area (mapping units and mapping unit classes).

As nearly as possible, the boundary lines between adjacent mapping units were located along visually observable lines of demarcation. Consequently, most of these boundaries represent marked differences in vegetational structure or composition or both. The boundary of each vegetational mapping unit was reconnoitered on foot or observed from some nearby vantage point. Once it was determined what the boundary should be, the proper lines were drawn on the outline map. Some boundaries could be traced directly from the aerial photographs. Others had to be located in reference to landmarks such as buildings, paths, etc.

OTHER DATA

The bulk of the data used in the following pages to describe the vegetation was provided by the vegetation surveys described above. Some quantitative data were obtained, however, from a study (page 29) which involved the measurement of cover and frequency by means of meter-square quadrats arranged contiguously along east-west transects. These data are included wherever possible. Likewise, a few measurements of environmental conditions (page 34) are also included in appropriate places.

RESULTS

The flora of Island Beach (Small & Martin 1958) includes at least 267 species of vascular plants representing 63 different families. Almost a third of these are ruderal weeds found only along the main highway and around building sites. Some are represented by a single plant, clone, or colony. Only two of the recently introduced species, *Carex kobomugi* and *Populus gileadensis*, show signs of becoming vegetationally important; both are well established and appear to be spreading rapidly.

Over half of the native species are also quite rare. Their populations are small, and often they are restricted to habitats of unusual character and infrequent occurrence. *Eleocharis parvula*, for example, occurs only on rotting organic deposits which occur only on the bay shore. These organic deposits consist of the dead parts of *Zostera marina* which are washed ashore by waves. The bulk of the vegetation is composed of about 75 abundant species which combine in various ways to produce many strikingly different kinds of vegetation cover.

Each mapping unit class (Table 4) represents a different kind of vegetation. The distribution of each kind of vegetation is shown by the vegetation map (Fig. 2). The chief purpose of the map is to show the kind of vegetation present in each area and the relative distribution of each kind of vegetation in the total area. The classification of mapping units is merely a device to aid in organizing the description of a complex vegetation in a complex environment. It is not an attempt to provide a "taxonomic" classification of plant communities or any other phytosociological units of vegetation.

Each mapping unit is labeled with one or a combination of symbols, and the meaning of each symbol is indicated in the map's legend. Each class of mapping units is described in the text in terms of its structural, compositional, and environmental characteristics. The mapping symbols and names of all mapping unit classes are listed in Table 4.

The quarter-mile check-points placed and numbered along the left margin of the map serve as a grid system. They are used in the text for convenience in referring to particular areas on the map. For example, "Fig. 2:5-7" refers to "Figure 2, the vegetation map, the stretch between check-points 5 and 7," and this indicates the approximate area between transects II and III.

22.

23.

24.

25. 6 Miles

26.

27.

28.

29. 7 Miles

30.

31.

32.

33. 8 Miles

34.

35.

36.

37. 9 Miles

38.

39.

40.

41. 10 Miles

BARNEGAT INLET
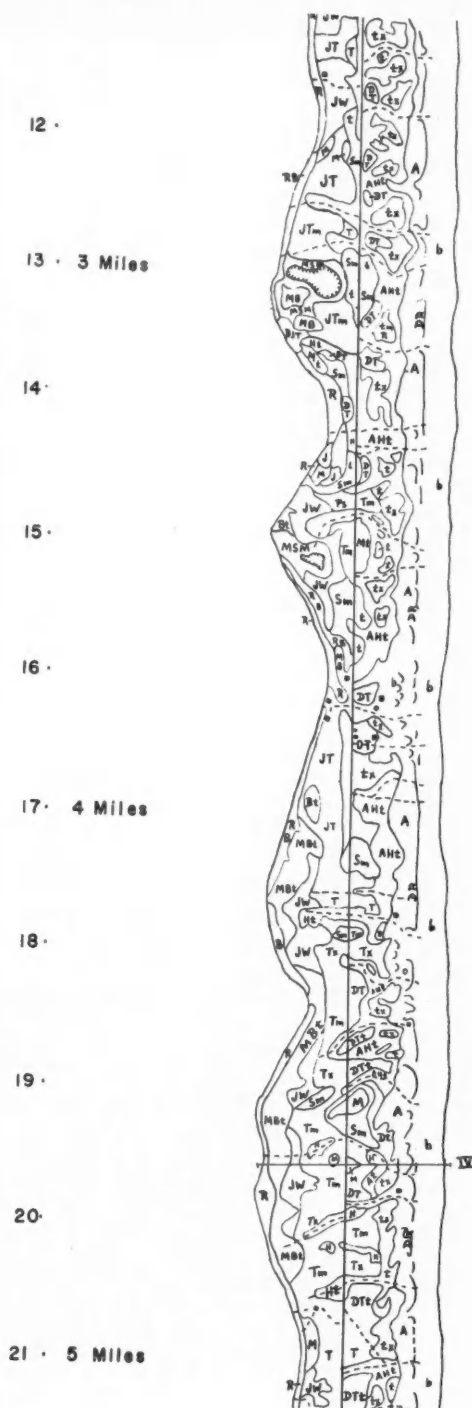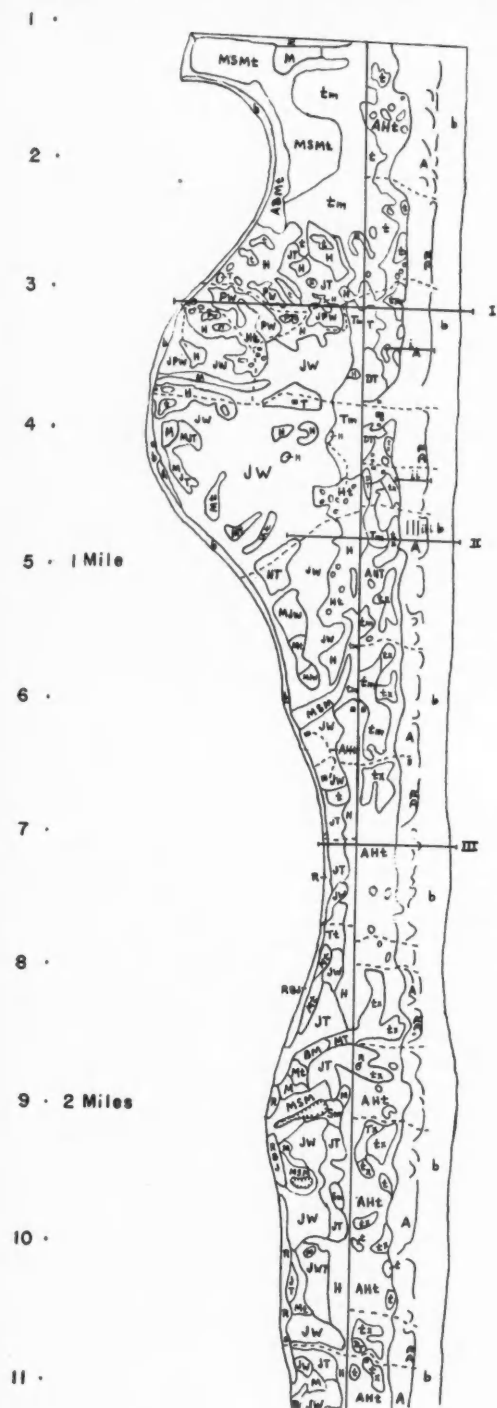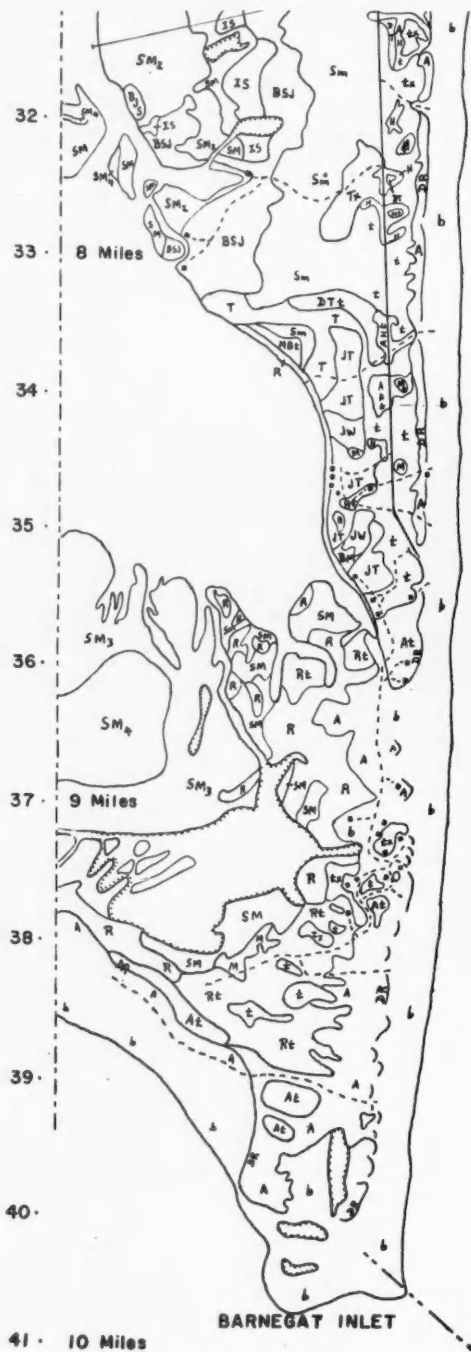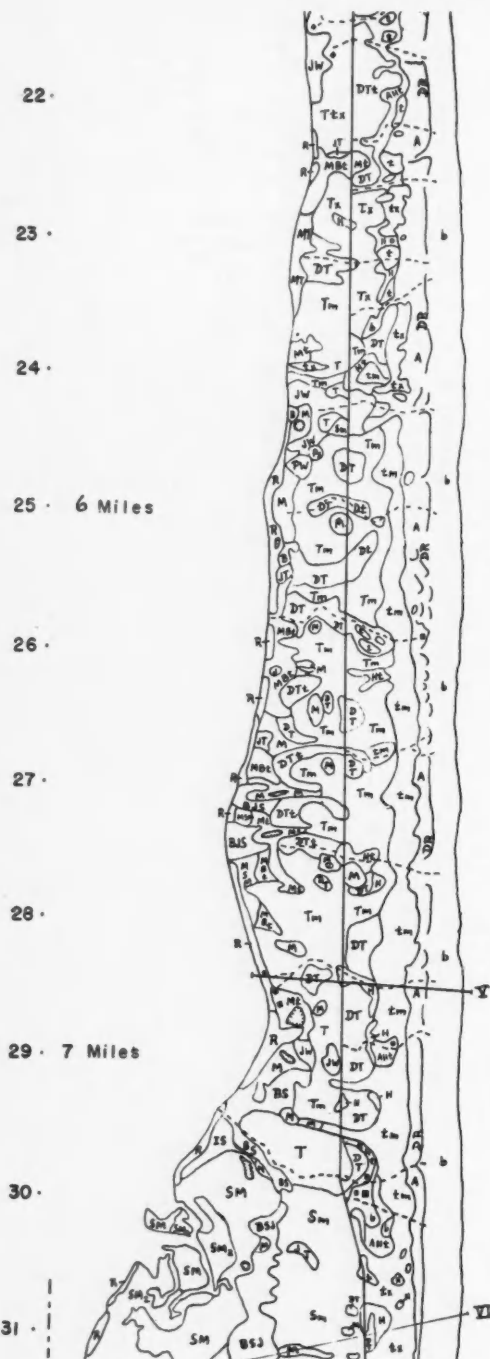
HERBACEOUS COMMUNITIES

The mapping units included in this group represent grasslands, marshy meadows, or xerophytic "heaths." The various community types represented by these mapping unit classes are composed largely of herbs or of subshrubs (chamaephytes) less than 1 ft in height. Taller shrubs and trees are usually absent. If present, they form an open to very sparse canopy which does not appear to reduce the herbaceous cover underneath.

1. *Dunegrass communities* (A)—Communities representing the Dunegrass community type are sparse grasslands (Fig. 3) of medium height. An analysis of 206 meter-square quadrats indicates an average vegetation cover of 8.4%; the remainder is bare sand.

FIG. 3. Dunegrass community on top of an active primary foredune, facing southeast during a northeasterly gale.

Ammophila breviligulata (dunegrass or marram grass) contributes 82% of the vegetation cover; *Solidago sempervirens* accounts for 12%. The remaining 6% is made up of species which are frequent in occurrence but not abundant. *Cakile edentula, Euphorbia polygonifolia, Lathyrus japonicus,* and *Artemisia stelleriana* show a high degree of fidelity.

Dunegrass communities are unusually uniform in regard to structure and composition, and their distribution is quite regular. Except for blowouts and one exceptionally stable dune occupied by *Carex kobomugi* (Small 1954), nearly all primary foredunes are occupied by Dunegrass communities.

Primary foredunes vary in height from 10 to 35 ft above mean sea level, and they are composed of siliceous sands and the roots and rhizomes of plants. These dunes are characterized by extreme environmental conditions: high exposure to windborne salt spray, marked deflation (wind erosion) and deposition, low moisture content, and extreme temperature fluctuations.

The Dunegrass community type is the only significant component of the herbaceous vegetation zone which is more or less coextensive with the topographic zone of primary foredunes. This herbaceous zone extends the full length of the bar, has an average width of about 50 m, and lies between the shore on the east and the shrubby zone on the west. In the northern sector of the park area (Fig. 2:1-9) and near the inlet (Fig. 2:36-40), this zone is very wide, and its western boundary is a gradual transition from Dunegrass communities to various kinds of Herb-Shrub Mixtures. In another area (Fig. 2:19-36), it is rather narrow, and its western boundary is an abrupt transition to Low Thicket of one kind or another. The greater width of this zone near the inlet and near the northern boundary of the park is associated with disturbance. As mentioned earlier, the inlet area was partly covered in 1954 with sand and shells dredged from the bottom of Barnegat Inlet. In 1932, a road was built from the northern boundary to Borough Hall (Fig. 2:1-6). This road was parallel to the shore and about 75 m inland from the primary foredune ridge. For most of its former length, it now lies buried beneath 5 to 10 ft of wind deposited sand.

2. *Beach Heather communities* (H)—The Beach

FIG. 2. The Vegetation of Island Beach State Park, N. J.

LEGEND
MISCELLANEOUS SYMBOLS

——— Main Highway and Transects		b	Beach, Bare Sand
- - - - - Sideroads and Footpaths		DR	Dune Ridge
- - - Jetty, ▮▮ Buildings		⬤	Ponds and Embayments
1-41 Quarter-mile check-points,		i-iii	Transects
used as a grid system		I-VI	Transects

VEGETATION MAPPING UNIT SYMBOLS

A	*Ammophila breviligulata*	D	Dune
B	*Baccharis halimifolia*		
H	*Hudsonia tomentosa*	M	Fresh Marsh
I	*Iva frutescens*	SM	Salt Marsh
J	*Juniperus virginiana*	t	Low Thicket, $<$ 7 feet
P	*Pinus rigida*	T	High Thicket, 7-15 feet
R	*Phragmites communis*	W	Woodland, $>$ 15 feet
S	*Spartina patens*	x	Xeric
Sm	*Smilax rotundifolia*	m	Mesic

Each mapping unit is labeled with one or a combination of the above symbols. Boundaries are based on Raynor Aerial Survey (1954) and on Vegetation Surveys (1956-57). Mapping unit symbols are listed in Table 4, and they are explained and described in the text.

TABLE 4. Classification of Vegetation Mapping Units.
The meaning of letters used in the mapping unit symbols
is explained in the legend of the vegetation map (Fig.
2). Numbers refer to sections in the text.

HERBACEOUS COMMUNITIES	1.	A	Dunegrass communities
	2.	H	Beach Heather communities
	3.	R	Reedgrass communities
	4.	M	Fresh Marsh communities
	5.	MSM	Brackish Marsh communities
	6.	SM	Salt Marsh communities
	7.	*	Cranberry Bog communities
LOW THICKETS	8.	t	Low Thickets
	9.	tx	Low Xeric Thickets
	10.	Dt	Low Dune Thickets
	11.	tm	Low Mesic Thickets
	12.	Sm	Greenbrier Thickets
	13.	Mt	Low Marsh Thickets
	14.	Bt	Low Sea Myrtle Thickets
HIGH THICKETS	15.	T	High Thickets
	16.	Tx	High Xeric Thickets
	17.	DT	High Dune Thickets
	18.	Tm	High Mesic Thickets
	19.	JT	High Red Cedar Thickets
	20.	*	High Red Cedar-Pine Thickets
	21.	MT	High Marsh Thickets
	22.	MJT	High Red Cedar-Marsh Thickets
	23.	BJT	Sea Myrtle-Red Cedar Thickets
HERB-SHRUB MIXTURES	24.	At	Dunegrass-Low T.M. (Thicket Mixtures)
	25.	Ht	Beach Heather-Low T.M.
	26.	HT	Beach Heather-High T.M.
	27.	HDt	Beach Heather-Low Dune T.M.
	28.	HDT	Beach Heather-High Dune T.M.
	29.	AHt	Dunegrass-Beach Heather-Low T.M.
	30.	Rt	Reedgrass-Low Shrub Mixtures
	31.	RB	Reedgrass-Sea Myrtle T.M.
	32.	RBJ	Reedgrass-Sea Myrtle-Red Cedar T.M.
	33.	BSJ	Salt Grass-Sea Myrtle-Red Cedar Savanna
	34.	BS	Salt Grass-Sea Myrtle Savanna
	35.	MMt	Fresh Marsh-Marsh T.M.
	36.	ABMt	Dunegrass-Sea Myrtle-Marsh T.M.
	37.	MSMt	Brackish Marsh-Marsh T.M.
	38.	MBt	Brackish Marsh-Sea Myrtle T.M.
	39.	IS	Salt Grass-Marsh Elder Savanna
TRANSITIONAL THICKETS	40.	Tt	High to Low Mesic Thickets
	41.	Ttx	High to Low Xeric Thickets
	42.	DTt	High to Low Dune Thickets
WOODLAND	43.	JW	Red Cedar Woodland
	44.	PW	Pine Woodland
	45.	JPW	Red Cedar-Pine Woodland
	46.	MJW	Swampy Red Cedar Woodland

*Not mapped.

FIG. 4. Beach Heather community (foreground), Low
Mesic Thicket (middleground)—note canopy sculptured
by salt spray, Red Cedar Woodland (background), fac-
ing west.

quency and fidelity but do not become abundant,
e.g., *Cladonia* spp., *Panicum amarum, Cyperus grayii,*
and *Lechea maritima.*

Beach Heather communities, like Dunegrass com-
munities, are quite uniform in structure and composi-
tion, but their distribution, in contrast, is rather
irregular. The principal Beach Heather habitats are
found on low, protected dunes in the primary and
secondary backdune areas at an average elevation of
9 ft above mean sea level. Because of excessive
drainage, most of these dunes are probably just as
xeric as those occupied by Dunegrass; but being better
protected from wind, they are less exposed to sand
movement and windborne salt spray.

In protected areas where the surface elevation is
generally higher than 6 ft (Fig. 2:3), Beach Heather
occupies the higher ground and surrounds the shrubby
or arborescent vegetation occupying the lower ground.
In protected areas where the elevation is generally
lower than 6 ft (Fig. 2:4), it occurs on isolated dune-
lets dispersed in a matrix of shrubby and arborescent
vegetation. Several dunelets too small to map sepa-
rately (Fig. 2:30) are occupied by Beach Heather
communities which are surrounded by marshy vege-
tation. Similar communities also occur in a few hab-
itats of moderate exposure such as the lower parts
of the seaward slopes of secondary foredunes. Beach
Heather is rarely encountered below 6 ft elevation,
and it is never found below 4 ft above mean sea level.

Beach Heather appears to be the chief pioneer
community (often long persistent) on protected and
inactive dunes. It may occur adjacent to Dunegrass
communities in some protected parts of the primary
backdune area, but it never competes with Dunegrass
on exposed or active primary foredunes.

3. *Reedgrass communities* (R)—Reedgrass com-
munities (Fig. 5) are tall, usually dense grasslands
composed chiefly of *Phragmites communis* (reedgrass)
which forms massive clones and sometimes grows to a
height of 8 ft or more. Below the level of the Reed-
grass "canopy", which is dense but because of its
structure does not cast a dense shadow, there may be

Heather community type is represented by commu-
nities (Fig. 4) of open, xeric, "heath." The leading
species is *Hudsonia tomentosa* (beach heather), a
chamaephyte of the Cistaceae, which forms low,
sprawling cushions that tend to spread radially along
the ground. The upright branches remain vigorous
year after year while the prostrate branches die back
regularly.

An analysis of 162 meter-square quadrats shows
70% bare sand or sand covered by dead branches of
Hudsonia tomentosa. Over 90% of the living vege-
tation cover (30% of the area) is contributed by
Hudsonia tomentosa. Most of the remainder is com-
posed of species which show a high degree of fre-

a scattered layer of shrubs including such species as *Rhus radicans*, *Juniperus virginiana*, *Baccharis halimifolia*, and *Rosa rugosa*. Sometimes there is a third layer which may include a large variety of hydrophytic grasses, sedges, forbs, and ferns.

FIG. 5. Reedgrass community on a sand ridge parallel to the bay shoreline. The narrow beach exposed at low tide is covered by a layer of dead and decaying eelgrass (*Zostera marina*) which grows on the bottom of the bay and is washed ashore by waves.

Reedgrass communities occur in habitats where they are well protected from salt laden winds but subject to a small amount of bay shore wave action and to infrequent tidal flooding. They may occupy marsh borders as a narrow band (Fig. 2:1) or a broad zone (Fig. 2:36-37), but they are much more common on sandy ridges which border the bay shore (Fig. 2: 8, 10, 20, etc.).

The low ridges of sand which commonly support Reedgrass communities are fashioned largely by the pushing action of ice which prevailing westerly winds cause to be piled up on the bay shore after sudden spring thaws. This is not an annual phenomenon (personal communication with John B. Verdier, Park Superintendent), but it occurs regularly whenever there are broken ice masses on Barnegat Bay. Ice-formed sand ridges are not found continuously along the bay shore; but, where they are found, they are almost always occupied by Reedgrass communities or some community which includes reedgrass among its dominant members.

Many of these ridges form natural dams which impede the drainage and prevent the tidal flooding of marshy areas. The marshes resulting from this process (see section #5) have unusual compositional and environmental characteristics.

4. *Fresh Marsh communities* (M)—The numerous Fresh Marsh communities of Island Beach are generally small in size, often less than 50 m in diameter. Most of them are similar in structure and occupy habitats of similar character, but the variation in their composition is considerable. Some of them are characterized by the dominance of one or a few species. Others are composed of numerous species none of which are obviously dominant. Between these two extremes, there appear to be a great many possible combinations of species in different orders of importance. Measurements of water table depth, ground water pH, ground water salinity, and substratum composition, however, failed to reveal any obvious environmental gradient along which these variations in composition might be arranged. An intensive analysis of many communities and their habitats would be necessary to determine whether the apparently contiuuous variation in the composition of these marsh communities should be attributed to chance differences in reproduction and migration and/or genetic differences which result in the regular arrangement of population patterns along environmental gradients.

A large number of species show a fairly high degree of fidelity to the communities included in the Fresh Marsh class of mapping units. It is not uncommon to find as many as 20 species in an area of 50 sq m. The following is a partial list of species which are abundant, show a high degree of fidelity, and have an estimated presence value of more than 30%: *Andropogon virginicus* v. *abbreviatus*, Carex spp., *Cyperus filicinus*, *C. odoratus*, *Dryopteris thelypteris*, *Eleocharis calva*, *Eupatorium album*, *Hibiscus palustris*, *Hypericum virginicum*, *Juncus canadensis*, *J. effusus*, *Oenothera perennis*, *Osmunda cinnamomea*, *O. regalis*, *Phragmites communis*, *Polygonum pensylvanicum*, *Scirpus americanus*, *Typha latifolia*.

Most Fresh Marsh communities are dense meadows of medium height (Fig. 6) composed of several to many species. Usually there is a small group of species which are more abundant than the others, but these combinations vary, and the member species of any particular combination are often about equal in importance. There are, however, 3 relatively simple combinations which recur frequently: (a) *Typha latifolia* is dominant in several marshes and forms a continuous stratum about 5 ft in height. An inferior herbaceous stratum about 1 ft in height is usually present and composed largely or entirely of *Dryopteris thelypteris*. (b) In other Fresh Marshes *Dryopteris thelypteris* may occur as the sole dominant, and it may form pure stands as much as 40 m in diameter. (c) *Hibiscus palustris*, because of its superior size and height, appears to be dominant in many fresh Marsh communities. It may form a discontinuous stratum 3 to 4 ft in height which overtops a lower stratum of rushes and forbs such as *Eleocharis calva*, *Scirpus americanus*, and *Hypericum virginicum*.

In one Fresh Marsh (Fig. 2:27) *Asclepias incarnata* is dominant; *Cyperus dentatus* is dominant in another area of similar size (Fig. 2:29); and another (Fig. 2:31) is composed of a nearly pure and exceptionally vigorous stand of *Spartina patens*. Many similar examples could be described in addition to these, but the full range of variation would still be largely unexplored.

There are only two characteristics held in common by all the communities designated as Fresh Marsh on the vegetation map. They are all meadows composed primarily of hydrophytic herbs, and they all occupy similar habitats.

FIG. 6. Fresh Marsh community surrounded by a Low Mesic Thicket. Identifiable species include: *Dryopteris thelypteris* and *Hibiscus palustris* in the foreground and *Scirpus americanus* in the background.

The habitats occupied by Fresh Marsh communities are: depressions, swales, hollows, washes, and low flats in which there is standing water for much of the year and the water table is rarely more than 12 in. below the surface. The substratum may vary from sand to peat or even muck. Ground water pH is less than 6.0 and ground water salinity is usually less than 5 parts per thousand. As will be demonstrated in a later section, these habitats are all less than 4 feet above mean sea level, and the transition from marsh to thicket vegetation (Fig. 6) is often associated with an increase in elevation of 1 ft or less.

As seen from the vegetation map (Fig. 2), Fresh Marsh communities are scattered throughout the central part of the bar, and they are usually surrounded by shrubby or arborescent vegetation. They are likely to occur anywhere that the surface elevation is sufficiently low and the drainage configuration is so arranged as to produce saturated soil conditions.

Shrubs are usually present in these communities, but areas in which the shrub cover is significantly large (45% or more) are relegated to other mapping unit classes. The most common shrubs in Fresh Marsh communities are: *Rhus radicans, Rosa rugosa,* and *Vaccinium corymbosum.* There is little doubt that Fresh Marsh communities can be replaced by Low Thicket communities which represent higher stages in hydrarch succession. These shrub communities (subsequent sections #13, 34, etc.) are also quite variable in composition.

5. *Brackish Marsh communities* (MSM)—Brackish Marsh communities are so designated because they are intermediate in composition between Fresh Marsh and Salt Marsh and because they occupy unique habitats.

An analysis of ground water samples collected in August, 1957, from different points in the same community indicates that the ground water salinity may vary from 3 to 20 parts per thousand. In response to occasional tidal flooding, evaporation during drought periods, and dilution by rainfall, the seasonal variation at any one point could be of an even greater magnitude.

The location, vegetational composition, and general character of the areas which have been designated as Brackish Marsh appear to be due, in large part, to the sand-ridging process described in section #3 above, in the discussion of Reedgrass communities. The formation of a complete sand ridge along the bay shore edge of a tidal-marsh either puts an end to tidal flooding or else it effectively reduces the frequency and severity of such flooding. With tidal flooding ended or reduced and the natural sub-surface drainage through sand under the salt peat only slightly impeded, it would appear that rainwater eventually washes the peat free or virtually free of soluble salts.

Water samples were collected from ponds surrounded by Brackish Marsh vegetation after a 2 month period in summer of virtually no precipitation. The maximum salinity (Fig. 2:9) was 7.5 parts per thousand and the minimum (Fig. 2:2) was 1.4. One would expect salinity to be at its highest at the end of such a period of drought. Compared with true tidal-marsh (section #6), these salinites are quite low.

Surface elevations and water table conditions are about the same as those reported for Fresh Marsh (section #5). The substratum, on the other hand, is salt peat from 0.5 to 3 ft in depth. In some places, this peat is covered with a mantle of sand, from 1 to 12 in. deep, which is thickest on the east and thinnest on the west side of marshes where it occurs.

The floristic composition of Brackish Marsh communities is variable in much the same fashion as described for Fresh Marsh. Many of the same species occur in both types, but the characteristic and often predominant species of Brackish Marsh is *Spartina patens,* the same species which is usually dominant in Salt Marsh communities. In Brackish Marshes it is accompanied by one, some, or all of the following: *Typha latifolia, Hibiscus palustris, Dryopteris thelypteris, Rhus radicans, Rosa rugosa,* or *Baccharis halimifolia,* which were never found in true tidal-marsh situations.

Brackish Marsh communities appear to be replaced by thicket communities in which *Baccharis halimifolia* (see myrtle) is abundant to very abundant (Sections #14, 23, 38, etc.). Being a characteristic species of tidal-marsh borders and bay shore sand ridges, it appears to have a sort of ecological priority in brackish habitats.

6. *Salt Marsh communities* (SM)—Salt Marsh or true tidal-marsh communities, which occur on Island Beach only in the southernmost 3-mi. segment (Fig. 2:20-41), are of four distinct types.

a. (SM) Typical Salt Marsh (Fig. 7) is a low, dense to open grassland composed principally of *Spartina patens.* An analysis of 87 meter-square quadrats, located entirely on transect VI (Fig. 2:31), shows that *Spartina patens* comprises 87% of the total vegetation cover while another 12% is contributed by *S. alterniflora.* The remaining 1% is com-

posed of halophytic chenopods such as *Salsola kali,* *Salicornia europaea,* and *S. virginica.*

FIG. 7. View facing east from 750 m on transect VI. Typical Salt Marsh (foreground), *Spartina alterniflora* in panne (middleground), and *Juniperus virginiana* (horizon) of Salt Grass-Sea Myrtle-Red Cedar Savanna.

Ground water salinity in this community varies from 23 to 26.6 parts per thousand. At the time of measurement, the salinity of bay water was 26.6 parts per thousand. The average elevation is 2.2 ft above sea level, and the average depth of peat is 2.1 ft.

b. (SM$_2$) *Salicornia virginica* is the most abundant species of an unusual community which occupies certain areas between the typical Salt Marsh and the bay. It forms a low, dense, perennial mat over typical salt peat. An analysis of 234 meter-square quadrats shows that slightly more than 74% of the total vegetation cover is contributed by *Salicornia virginica,* about 20% by *Spartina alterniflora,* and a little less than 6% by *S. patens.*

At any one time, ground water salinity may vary from 30 to 36 parts per thousand at different points in the same community. Salinities considerably higher than that of bay water suggest a concentration of ground water by surface evaporation. This interpretation is also in line with the observation that most of the Salt Marshes on Island Beach are not flooded by every tide but only by the higher high tides. The average elevation of this community above mean sea level is 1.9 ft or 0.3 ft lower than that of typical Salt Marsh. (The mean water level in the bay is somewhat above mean sea level.) The average depth of peat is 1.8 ft.

c. (SM$_3$) One large island adjacent to the southern end of the bar (Fig. 2:35-37) is occupied by a Mosaic Salt Marsh. For the most part, this vegetation is a low, open to sparse grassland in which areas dominated by one species or a combination of a few species alternate with areas dominated by other species or other combinations of species

Flat areas having the highest apparent elevation tend to be occupied by *Distichlis spicata,* intermediate areas by *Spartina patens,* and the lowest areas by stunted *Spartina alterniflora.* Pannes are numerous in this area. Some are water-filled and barren of plants while others are drier and occupied by halophytic forbs, especially *Salicornia europaea.*

Salinity varies from 25 to 33 parts per thousand. The average elevation, which is very little different from that of tidal-marshes on the bar, was not determined, but the average depth of peat is less than 1.0 ft.

d. (SM$_4$) One rather large area of lower elevation in the center of the island mentioned above supports only a few scattered and depauperate plants of *Spartina alterniflora.* This area resembles nothing more than a large panne. Ground water salinity, at the time of measurement in August, was 30-42 parts per thousand. The substratum consists of a hard crust of surface peat about 3 in. thick, a layer of soft organic material which varies from 1 to 8 in., and another very thin, hard crust which is underlain by a mixture of sand and fine, dark-colored silt.

The data collected during reconnaissance and survey studies seem to indicate a close relationship between the composition of Salt Marsh vegetation, microrelief, and salinity. A more intensive study of the influence of microrelief, tidal action, rainfall, and vegetation on salinity differences and changes is needed for a better understanding of these relationships.

Regular zones of thicket vegetation (sect. #33) occur parallel to the inner margin of the largest Salt Marsh area (Fig. 2:30-33), but these do not necessarily represent stages in biotic succession. The conversion of Salt Marsh to some other kind of vegetation appears to depend on physiographic processes which bring about environmental changes. The action of ice moved by wind (sect. #3, 5) is one example of such a process; others will be considered later.

7. *Cranberry Bog communities* (*)—Cranberry Bogs form a very small part of the vegetation complex, and the areas occupied by them are not large enough to be mapped separately.

A typical Cranberry Bog is composed principally of *Vaccinium macrocarpon* (large cranberry), a trailing chamaephyte, which virtually covers the ground. Sphagnum moss is usually present and sometimes very abundant. *Lycopodium inundatum* and *Drosera filiformis* or *D. rotundifolia* are almost always present. *Juncus effusus* may be sufficiently abundant to form a sparse, overtopping herb stratum. *Pogonia ophioglossoides* and *Oenothera perennis* are infrequent but characteristic members of this community type.

Most Cranberry Bogs are found in hollows which are located between secondary backdunes or immediately to the west of secondary foredunes and have surface elevations between 3 and 4 ft above mean sea level.

LOW THICKETS

The mapping unit classes included in this group represent Low Thicket communities composed of shrubs, tree saplings, and/or lianas which form a canopy whose average height is no more than 7 ft. The total shrub cover in areas mapped as Low Thicket

is 50% or more on xeric sites and usually 75% or more on mesic sites. Herbaceous cover may occur in openings, but it is usually absent or meagerly developed under dense shrub cover.

8. *Low Thicket* (t)—The symbol "t" is used on the vegetation map in all combinations that signify an abundance of shrubs, tree saplings and/or lianas less than 7 ft in height. When used alone, it designates an area which is occupied by Low Thicket; but because of its small size or unusual composition, it cannot be placed in any of the more sharply defined categories which follow.

9. *Low Xeric Thicket* (tx)—Areas mapped as Low Xeric Thicket may vary somewhat in composition and structure. A "typical" area of Low Xeric Thicket (Fig. 8) is a dense, virtually impenetrable, nearly flat-topped mass of crowded shrubs with a generous interlacing of thorny lianas.

FIG. 8. View facing east from about 200m at Fig. 2:31. The Dunegrass community is visible on the backslope of a primary foredune (background), "typical" Low Xeric Thicket grades into High Xeric Thicket which is barely visible in the lower left corner.

Rhus radicans, Myrica pensylvanica, Prunus serotina, Juniperus virginiana, Smilax rotundifolia, and *Parthenocissus quinquefolia* are the most abundant and most characteristic species of shrubs, trees, and lianas. They ocur in almost all of the areas mapped as Low Xeric Thicket. An analysis of 220 meter-square quadrats indicated a total shrub cover of 77%. Over 60% was contributed by the 6 species listed above. The remaining 17% was contributed by species which are also characteristic of xeric sites but which occurred in these quadrats with a frequency of less than 5%. Characteristic but infrequent species include the following: *Quercus ilicifolia, Prunus maritima, Ilex opaca, Rhus copallina Amelanchier canadensis* and *Rosa virginiana.*

In the same quadrats, the herbaceous cover was less than 6%. *Smilacina stellata,* which occurred with a frequency of only 5%, provided an herbaceous cover of 3.5%. *Ammophila breviligulata* and *Solidago sempervirens* were the only other herbaceous species to occur with a frequency of over 3%.

The characteristic habitat for Low Xeric Thicket is a high primary backdune swale lying between the primary and secondary foredunes. It does not, however, form a continuous zone comparable to the Dunegrass zone. For most of the length of the bar (Fig. 2:1-24), it occurs as thicket-islands in a matrix of various kinds of herb-shrub mixtures. In one area (Fig. 2:24-30), it is virtually absent, and in the southern sector (Fig. 2:30-41), it is poorly developed. The best developed area of such vegetation (Fig. 2:24) is illustrated in Figure 8.

Transect studies indicate that the average elevation of Low Xeric Thicket habitats is 7.5 ft above mean sea level or about 5 ft higher than the average elevation of the water table. Exposure to salt spray varies from high along the seaward edge to moderate at canopy height farther inland to negligible below the canopy level. Some areas of this kind of vegetation (Fig. 2:12, 18) have been buried recently by an accumulation of sand along their seaward borders.

10. *Low Dune Thicket* (Dt)—The structure and composition of vegetation mapped as Low Dune Thicket differs somewhat from that of Low Xeric Thicket, but the important difference is that of habitat.

An analysis of 68 meter-square quadrats in 5 different areas of Low Dune Thicket indicates a total shrub cover of only 58%. *Parthenocissus quinquefolia, Prunus serotina,* and *P. maritima* account for nearly 50%. The remaining 8% is made up mostly of *Rhus radicans, Myrica pensylvanica, Smilax rotundifolia,* and *Juniperus virginiana.* The herbaceous cover is very sparse.

Low Dune Thicket occurs on the exposed eastern or seaward slopes and tops of secondary foredunes and transverse ridges (Fig. 2:25). As might be suspected, most of the areas occupied by this open kind of low thicket are too small to be mapped separately.

11. *Low Mesic Thicket* (tm)—*Vaccinium corymbosum* (highbush blueberry) is the most abundant species in the areas mapped as Low Mesic Thicket. Most thickets of this kind (Fig. 4) have a nearly flat-topped canopy broken only by the salt-spray-sculptured crowns of a few transgressives.

An analysis of 87 meter-square quadrats indicated a total shrub cover of 102%. (Due to the summation of the percentage cover of overlapping species, total cover in dense vegetation is often more than 100%.) *Vaccinium corymbosum* accounted for 55%, *Rhus radicans*—15%, *Kalmia angustifolia*—8%, and *Smilax rotundifolia*—7%. The remaining 15% was made up of *Myrica pensylvanica, Amelanchier canadensis, Rhus copallina, Rosa rugosa, Prunus serotina,* and *Parthenocissus quinquefolia.* The sparse herbaceous stratum was made up chiefly of three species of ferns: *Dryopteris thelpteris, Osmunda cinnamomea,* and *O. regalis.* Sphagnum moss, *Vaccinium macrocarpon,* and a few forbs were also present in small openings. In other examples of this community type, the herb and moss strata are more dense and more varied in composition; in some they are entirely lacking.

The two communities which provided the data

listed above both occupy flat-surfaced depressions within 15 in. of the water table. Their borders were surveyed with a theodolite level and found to conform remarkably well to a contour line between 4 and 5 ft elevation. *Vaccinium corymbosum* was nowhere encountered on a site known to be more than 5 ft above sea level.

Low Mesic Thickets occur in the same general zone described for Low Xeric Thicket. The mesic form appears to be restricted to hollows or swales which are low enough to be near the water table but not low enough to have standing water for extended periods during the growing season. They are exposed, at canopy height, to considerable amounts of salt spray, but they are not generally exposed to burial by sand. The best developed area of Low Mesic Thicket (Fig. 2:24-30) occupies a long, low swale immediately inland from a well-stabilized primary foredune ridge.

12. *Greenbrier Thicket* (Sm)—*Rhus radicans, Myrica pensylvanica,* and *Smilax rotundifolia* (greenbrier) are important species in all low thicket areas. Several large, mesic areas are dominated by greenbrier. These areas (Fig. 2:15, 17, 19, 30-33) have been mapped as Greenbrier Thicket. The vegetation of these areas is a dense tangle of greenbrier which grows alone or over the dead skeletons of shrubs and forms a springy "mattress" about 6 ft deep.

An analysis of 156 meter-square quadrats indicates a vegetation cover which, due to overlapping, totals 108%. *Smilax rotundifolia* accounts for 94%. The remainder is made up of *Rhus radicans* and *Parthenocissus quinquefolia,* which grow among the vines of the dominant, and the following shrubs and trees which support or rise above the tangle of greenbrier: *Vaccinium corymbosum, Ilex opaca, Juniperus virginiana, Rhus copallina, Amelanchier canadensis,* and *Prunus serotina.*

The habitats occupied by these communities vary from 4 to 10 ft above mean sea level. The average elevation is 6 ft. This suggests a habitat which is not quite as mesic as that of Low Mesic Thicket nor as xeric as that of Low Xeric Thicket.

13. *Low Marsh Thicket* (Mt)—Low Marsh Thicket communities are usually stratified. The shrub stratum is less than 7 ft high on the average and covers more than 50% of the ground. The herb stratum is irregular in structure and composition, usually discontinuous, and covers less than 50% of the ground. The composition of both shrub and herb strata exhibits roughly the same range of variation as described earlier for Fresh Marsh communities.

The most common and frequently most important shrub species are those which are more or less ubiquitous in their distribution. Included in this group are: *Rhus radicans, Myrica pensylvanica,* and *Juniperus virginiana.* Species which are perhaps more characteristic and have a higher degree of fidelity include the following: *Acer rubrum, Rosa rugosa, Baccharis halimifolia,* and *Pyrus arbutifolia.*

An analysis of 48 meter-square quadrats from parts of four separate but similar communities provides an indication of the composition. The herbaceous cover, composed equally of *Dryopteris thelypteris* and *Juncus canadensis,* totals 45%. The total shrub cover is 90% and constituted as follows: *Rhus radicans*—33%, *Acer rubrum*—15%, *Rosa rugosa*—10%, *Baccharis halimifolia*—10%, *Myrica pensylvanica*—8%, and *Juniperus virginiana*—4%.

Low Marsh Thickets usually occur around the margins of Fresh Marshes. Habitats which are occupied exclusively by Low Marsh Thicket appear to be environmentally equivalent to those occupied exclusively by Fresh Marsh. The composition of the herb stratum and the occurrence of numerous communities which are intermediate in structure and composition (sect. #35), leaves little doubt that Fresh Marsh communities are replaced by Low Marsh Thicket communities.

14. *Low Sea Myrtle Thickets* (Bt)—Only two examples of this community type (Fig. 2:15 and 17) have been mapped. *Baccharis halimifolia* (sea myrtle) is usually found in Brackish Marsh habitats, but in these two examples, it forms a dense canopy over an herb stratum which is quite representative of Fresh Marsh. Salinity tests were negative. (For other Sea Myrtle thicket types, see sect. #23, 31, 32, 33, 36, 37.)

HIGH THICKETS

High Thickets are plant communities composed almost entirely of shrubs, trees, and lianas forming a more or less level-topped canopy which is between 7 and 15 ft in average height. The distinction between High Thicket and Low Thicket is made because of a shift in composition which appears to be correlated with a canopy height of about 7 ft. This approaches the maximum potential height of all but a few individuals of several shrub species. Under higher canopies, these species are suppressed; and consequently, tree species, capable of attaining a greater maximum stature, assume a greater importance. Inferior shrub strata of uniform structure and composition are uncommon in these communities, and herb strata are absent or poorly developed.

15. *High Thicket* (T)—The symbol "T" is used on the vegetation map in all combinations that signify an abundance of shrubs, trees, and/or lianas between 7 and 15 ft in height. When used alone, it signifies an area which is occupied by High Thicket; but because of its small size or unusual composition, it cannot be placed in any of the more sharply defined categories which follow.

16. *High Xeric Thicket* (Tx)—Only a few areas (Fig. 2:18-24) have been mapped as High Xeric Thicket. In these areas, the canopy is about 12 ft high and virtually level except for occasional emergent trees of *Juniperus virginiana.* In these communities, the stems of trees and shrubs are close-spaced and so interlaced with lianas that they present a virtually impenetrable barrier.

The canopy is composed of *Juniperus virginiana, Ilex opaca, Prunus serotina,* and *Amelanchier cana-*

densis which are the chief tree species of Low Xeric Thicket. Also present, in the canopy but generally of lesser importance are *Quercus marilandica, Q. falcata,* and *Sassafras albidum. Rhus radicans* and *Smilax rotundifolia* are the principal lianas, and they grow with their leaves among those of the trees. Also present but generally suppressed and not reaching the canopy level are: *Myrica pensylvanica, Quercus ilicifolia,* and *Prunus maritima.*

Similar communities of smaller size are found (but not mapped) in protected places all along the inland edge of Low Xeric Thicket. The obvious inference is that these communities represent later stages in the successional development of Low Xeric Thicket. The shift in composition appears to be due to the ascendancy of trees over shrubs.

17 *High Dune Thicket* (DT)—High Dune Thickets (Fig. 9) have a continuous canopy of *Prunus serotina* (black cherry) which salt spray keeps pruned level with the dunes on whose backslopes they occur. A 26 m transect through one such community (Fig. 2: transect VI) indicated a total woody cover of 108%.

FIG. 9. Facing east from 250m on transect VI, High Dune Thicket on backslope of secondary foredune, note defoliated twigs of current season's growth and levelness of the canopy.

Prunus serotina accounted for 83% of this, and the remainder was contributed by *Ilex opaca, Myrica pensylvanica, Parthenocissus quinquefolia,* and *Rhus radicans.*

Communities of this kind are virtually restricted to the backslopes and salt spray shadows of secondary foredunes. A few clumps of *Prunus serotina* are found, however, on the backslopes of primary foredunes. Such clumps are relatively common in areas (Fig. 2:24-30) where the backslopes of primary foredunes are steep but well stabilized by *Rhus radicans.*

18. *High Mesic Thicket* (Tm)—Most of the large areas mapped as High Mesic Thicket (Fig. 10) are very dense, often dominated by *Vaccinium corymbosum,* and have a canopy height of about 10 ft. Certain shrub species—*Rhus radicans, Kalmia angustifolia, Smilax rotundifolia,* etc.—which are associated with *Vaccinium corymbosum* in Low Mesic Thicket, are also present in the higher counterpart, but they are much reduced in importance. As shown below, several tree species are much increased in importance.

An analysis of 109 meter-square quadrats indicates a total crown cover of 112%. In some areas

FIG. 10. Cross-section of High Mesic Thicket made by a recent road cut near Fig. 2:28, note extreme density and slight slope of canopy, right side of picture is east, line at base of grader throw is about level, and the stake (lower right) is about 1 ft high.

(see Figure 10), it is even more dense. *Vaccinium corymbosum* accounts for 48% of this total. Also present in the upper canopy are *Ilex opaca*—13%, *Juniperus virginiana*—12%, *Acer rubrum*—12%, and a few scattered individuals of *Sassafras albidum, Amelanchier canadensis, Rhus copallina,* and *Myrica pensylvanica.* The poorly developed, low shrub stratum (approximately 25% cover) is composed of *Rhus radicans, Myrica pensylvanica, Rosa rugosa,* and *Kalmia angustifolia.* The meagerly developed herb stratum (less than 10%) includes *Dryopteris thelypteris, Osmunda cinnamomea,* and *O. regalis.*

Different species are involved, but the shift in importance from shrub species in Low Mesic Thicket to tree species in High Mesic Thicket is similar to that already described for their xeric counterparts. It is logical to infer that the same processes are involved in both cases, but the processes themselves have not been fully established.

The habitats occupied by High Mesic Thicket are similar in elevation and other respects to those occupied by Low Mesic Thicket, but they are located farther inland from the shore or on sites which are less exposed to salt-laden ocean winds. In a few places (Fig. 2:23-24), there is a gradual transition from Dunegrass communities on the high dunes adjacent to the shore to Low Xeric Thicket to Low Mesic Thicket and, finally, to High Mesic Thicket at a distance of about 300 m from the ocean shoreline. This kind of gradation represents the kind of "regular zonation" which might be expected on theoretical grounds, but it is rarely encountered in the field.

19. *High Red Cedar Thicket* (JT)—These are dense thickets, 7 to 15 ft in height, dominated by *Juniperus virginiana* (red cedar) which comprises 35% or more of the canopy. This percentage might be higher, but *Juniperus virginiana* often has a spire-shaped crown and rarely forms a closed canopy. The spaces between the taller trees are occupied by High Xeric Thicket or High Mesic Thicket having virtually the same composition as described above (sect. #16, 18). Also present, but less important,

in the canopy are: *Ilex opaca, Prunus serotina*, and *Amelanchier canadensis.*

The undergrowth of the community is a dense tangle of shrubs and lianas, but there is little uniformity in its composition as it varies from one site to another. The main reason for recognizing High Red Cedar Thicket as a separate mapping unit class is to show the location of areas in which *Juniperus virginiana* has gained or is gaining ascendancy over the lower shrubs and less resistant or slower growing trees. Since the highest (tallest and apparently nearest to climax) communities on Island Beach are low woodlands (sect. #43-46) dominated by *Juniperus virginiana* or *Pinus rigida*, these areas of High Red Cedar Thicket are implicated, by inference, as subterminal or intermediate stages in autogenic succession. The variable character of the understory, and its resemblance both to xeric and to mesic thicket types, suggests a convergence of xerosere and hydrosere.

The areas mapped as High Red Cedar Thicket occur along the borders of Red Cedar Woodland (Fig. 2:3, 9-10), or else they alternate with smaller areas of Red Cedar Woodland (Fig. 2:7-21, 34-36). They are all situated in secondary backdune areas which lie 300 m or more west of the ocean shoreline. Some of them occupy mesic habitats, and some occupy more xeric habitats. Where their seaward borders are exposed to salt-laden winds, they show signs of severe salt spray injury and pruning.

20. *High Red Cedar-Pine Thicket* (*)—High thickets which are dominated equally by *Juniperus virginiana* and *Pinus rigida* (pitch pine) occur only at the junction of Red Cedar Woodland and Pine Woodland (Fig. 2:3-4) and around the edges of a few areas which have been mapped as Red Cedar-Pine Woodland (Fig. 2:3-4). None of these areas are large enough to be mapped separately.

21. *High Marsh Thicket* (MT)—This mapping unit class was set up to indicate the stratified communities which occur in a narrow, discontinuous band around the margins of most Low Marsh Thicket communities. Only one area of this type (Fig. 2:8-9) was found to be large enough to map separately. The herb stratum, made up largely of *Dryopteris thelypteris*, is like Fresh Marsh. The low shrub stratum, composed of *Rosa rugosa*, is like Low Marsh Thicket, and the high shrub stratum, composed of *Acer rubrum* and *Vaccinium corymbosum*, is like High Mesic Thicket.

22. *High Red Cedar-Marsh Thicket* (MJT)—Only one sizable area (Fig. 2:4) was mapped to indicate this kind of vegetation. In this particular area, the herb stratum is a mixture of Fresh Marsh species in which *Hibiscus palustris* and *Eleocharis calva* are especially noticeable. The low shrub stratum is composed mostly of *Rhus radicans*, but it also contains *Rosa rugosa* and *Pyrus arbutifolia*. The high shrub stratum is made up of *Juniperus virginiana* and *Acer rubrum.*

23. *Sea Myrtle-Red Cedar Thicket* (BJT)—This

is another mapping unit class which was used only once (Fig. 2:13-14). It indicates a very dense thicket about 10 ft in height which is composed almost exclusively of *Baccharis halimifolia* and *Juniperus virginiana* which form a canopy so dense that very few plants grow in the dense shade beneath it. A few plants of *Dryopteris thelypteris* and *Osmunda cinnamomea* together with scattered individuals of *Rosa rugosa* and *Pyrus arbutifolia* indicate affinities with Fresh Marsh (or Low Mesic Thicket) and Low Marsh Thicket.

HERB-SHRUB MIXTURES

Most of the mapping unit classes included in this group indicate areas of complex vegetation which are intermediate in structure and composition (and probably in successional status) between one or several community types of a more uniform character. The outstanding characteristic of the community types included in this group is that their total vegetation cover is composed of about equal proportions of herbs and shrubs. Most of these mapping units represent one or both of two intergrading kinds of structure, but no attempt has been made to distinguish one from the other on the vegetation map.

One kind of structure indicated by most of these mapping unit classes can be designated as "shrub savanna"; the other and perhaps more prevalent kind of cover is referred to as "herb-shrub complex." Shrubs in the shrub savanna type occur as evenly-spaced individuals, small clones, or small clumps dispersed in a nearly continuous matrix of herbs or subshrubs or both. In the herb-shrub complex type of vegetation cover, shrubs occur as small thicket communities surrounded by or alternating with communities composed of herbs or subshrubs or both. While the individual communities are easy to recognize, they are too small to be mapped separately.

24. *Dunegrass-Low Thicket Mixture* (At)—Mixtures of Dunegrass and Low Thicket communities occur with considerable regularity along the border between the Dunegrass zone and the shrubby zone. These transitions are usually rather narrow and do not occupy areas large enough to be mapped separately. In the southern sector of the bar, however, a few areas of considerable size (Fig. 2:35-41) are occupied by this kind of vegetation.

The composition of the herbaceous stratum is virtually identical to that of Dunegrass communities on active dunes, but the density of *Ammophila breviligulata* is about twice the average for the Dunegrass community type. Shrubs, occurring as individuals, clumps, or small clones, comprise 10-50% of the total vegetation cover. The leading shrub species are those which characterize Low Xeric Thicket: *Rhus radicans, Myrica pensylvanica, Smilax rotundifolia*, and *Parthenocissus quinquefolia.*

The typical habitats for this kind of vegetation cover are found on the backslopes of active dunes or on xeric dune expanses at a greater distance from the primary foredune ridge. These habitats differ

from those of the primary foredune ridge in that they are somewhat less exposed to wind and hence to salt spray and sand movement. Because of their lower average elevation, they may be a little less xeric. Given a sufficient amount of time and freedom from disturbance, it is probable that these areas will develop into Low Xeric Thickets similar to those described in Section #9.

25-28. *Beach Heather-Thicket Mixtures* (Ht, HT, HDt, HDT)—It was suggested in section #2 that the pioneer vegetation in xerarch succession on inactive dunes is represented by the Beach Heather community type. Beach Heather-Thicket Mixtures of at least four different kinds occur in habitats which are virtually identical to those occupied by typical Beach Heather communities.

An analysis of 200 meter-square quadrats shows that the total herb cover in areas occupied by Beach Heather-Low Thicket (Ht) mixtures is about 16%. *Hudsonia tomentosa* (beach heather), *Andropogon scoparius* var. *littoralis*, and *Panicum amarum* account for 14% of this. The total shrub cover recorded in the same quadrats was 15%, and this was made up of 9 species of about equal importance: *Prunus maritima, Ilex opaca, Rhus radicans, Pinus rigida, Sassafras albidum, Quercus ilicifolia, Myrica pensylvanica, Juniperus virginiana, Smilax rotundifolia,* and *Rubus flagellaris.*

Beach Heather-High Thicket mixtures (HT) differ in that tree species such as *Juniperus virginiana, Prunus serotina,* and *Quercus marilandica* are more important than shrubs. The only sizable area of this kind of vegetation cover (Fig. 2:5) is found along a footpath.

Mixtures of Beach Heather and Low or High Dune Thicket (HDt, HDT) occur only on the foreslopes and tops of some secondary foredunes, on transverse ridges, and along footpaths. For the most part, these areas are small and have not been mapped separately. They differ from Low and High Dune Thicket previously described (sect. #10, 17) only in the fact that there is an "herb" stratum of *Hudsonia tomentosa* and that the total shrub cover is generally estimated to be less than 50%.

29. *Dunegrass-Beach Heather-Low Thicket Mixture* (AHt)—The vegetation cover of areas included in this mapping unit class varies from that of a relatively uniform Dunegrass-Shrub savanna (Fig. 11) to that of a highly heterogeneous herb-shrub complex in which small areas dominated by *Ammophila breviligulata* and its associated species alternate with small areas occupied by *Hudsonia tomentosa* and its associates, and other areas of Low Thicket.

An analysis of 96 meter-square quadrats indicates a total herb cover of 12% and a total woody cover of 45%. Since there is very little overlapping of herbs and shrubs, the remainder of the area, about 43%, is bare. Included among the herbaceous species are *Ammophila breviligulata* and its associates: *Solidago sempervirens, Artemisia stelleriana,* and *Euphorbia polygonifolia;* and *Hudsonia tomentosa* and its as-

FIG. 11. Facing east at Fig. 2:2, Dunegrass-Shrub Savanna in a low primary backdune swale (foreground) and Dunegrass-Beach Heather-Low Thicket Mixture on irregular primary backdune. The whole area is mapped as *AHt* (Sect. #29).

sociates: *Cyperus grayii, Panicum amarum,* and *Lechea maritima.* The leading shrub species are: *Rhus radicans, Myrica pensylvanica, Smilax rotundifolia,* and *Parthenocissus quinquefolia* which account for 35% of the shrub cover. The remaining 10% is made up of *Rosa virginiana, Juniperus virginiana, Ilex opaca, Prunus maritima,* and *Amelanchier canadensis.*

These figures are probably typical for most of the areas mapped as Dunegrass-Beach Heather-Low Thicket, but a complete listing of species would include nearly all of the species previously listed for Low Xeric Thicket (sect. #9) and High Xeric Thicket (sect. #16).

The habitats occupied by this mixture are found between the primary and secondary foredunes at elevations well above the water table. The Dunegrass-Shrub savanna, however (Fig. 11), is found only on relatively mesic sites. Interrupted only by larger, compact areas of Low Thicket, and bordered on the east by the Dunegrass zone, this zone of Dunegrass-Beach Heather-Low Thicket extends for half the length of the bar (Fig. 2:1-20), and its average width is approximately 125 m.

30. *Reedgrass-Low Shrub Mixture* (Rt)—Areas mapped as Reedgrass-Low Shrub mixtures are confined to the southern part of the bar (Fig. 2:37-39). The vegetation indicated by this class of mapping units is an open stand of *Phragmites communis* (reedgrass) over 6 ft high on its western edge and grading to less than 3 ft high on its eastern edge where it is bordered by *Ammophila breviligulata.* Contained in these areas are several large clumps of Low Thicket and numerous scattered shrubs, especially *Myrica pensylvanica, Rhus radicans* and *Smilax rotundifolia.*

The habitat occupied by this community is an artificial one produced by covering marshes, mud flats, and thickets with sand dredged from the bottom of Barnegat Inlet in 1954. From a high point of about 15 ft near the ocean shore, this area slopes inland to a low point of about 2 ft near the bay shore. The xeric portions of this disturbed area are occupied by *Ammophila breviligulata* and the more mesic portions by *Phragmites communis.* Small thicket areas sur-

rounded by mixtures of reedgrass and low shrubs appear to be remnants of larger thickets which were not entirely covered by dredge discharges.

31. *Reedgrass-Sea Myrtle Mixture* (RB)—Reedgrass communities described earlier (sect. #3) commonly have an inferior shrub layer below the canopy of *Phragmites communis*. In time, some of these shrubs become as tall as the grass. Areas dominated by *Phragmites communis* but having a "canopy" cover of at least 25% *Baccharis halimifolia* (Fig. 2:12, 17) are mapped as Reedgrass-Sea Myrtle mixtures. *Juniperus virginiana*, *Rhus radicans*, and *Rosa rugosa* are usually present beneath the grass-shrub "canopy."

The habitats occupied by these communities are the same in character as those occupied by typical Reedgrass communities. The inferred successional relationship between the two communities is apparent.

32. *Reedgrass-Sea Myrtle-Red Cedar Savanna* (RBJ)—Two areas of this kind of vegetation have been mapped (Fig. 2:8-9). The total woody cover in these two communities is about 50%: 25% *Baccharis halimifolia* (sea myrtle) and 25% *Juniperus virginiana*. Otherwise, they are no different from the more numerous areas mapped as Reedgrass-Sea Myrtle mixtures (sect. #31).

33. *Salt Grass-Sea Myrtle-Red Cedar Savanna* (BSJ)—The best developed examples of this kind of vegetation occur (Fig. 2:30-33) along the inner borders of the principal Salt Marsh areas. This stratified community (Fig. 12) has a nearly continuous herb stratum which is composed chiefly of *Spartina patens* (salt grass), a discontinuous shrub stratum in which *Baccharis halimifolia* is the leading species, and an overstory of widely-spaced *Juniperus virginiana*.

FIG. 12. Facing northwest at 550m on transect VI, Salt Grass-Sea Myrtle-Red Cedar Savanna, recognizable species are: *Spartina patens* (grass), *Rhus radicans* (low shrub), *Baccharis halimifolia* (high shrub) and *Juniperus virginiana* (evergreen tree).

An analysis of 118 meter-square quadrats on transect VI (Fig. 2:31) indicates a total herb cover of 83% and a total woody cover of 69%. *Spartina patens* contributes 76% of the herb cover; the remainder is composed principally of *Panicum virgatum, Andropogon scoparius* var. *abbreviatus*, and

Vulpia octoflora. The woody cover is made up of *Baccharis halimifolia*—36%, *Rhus radicans*—14%, and *Juniperus virginiana*—10%. The remaining 9% is composed of *Myrica pensylvanica, Rhus copallina*, and *Acer rubrum*.

The habitat is relatively flat-surfaced and has an average elevation of 3.1 ft above mean sea level. The substratum is sand from 12 to 24 in. in depth overlying peat which averages 25 in. in thickness. Ground water salinity varies from 4 to 10 parts per thousand and pH from 4.5 to 7.1. Salt spray damage to twigs and foliage is slight, and the only plants affected are a few of the taller individuals of *Juniperus virginiana*.

From the nature of the substratum and the position of the largest area of this kind of vegetation (Fig. 2:30-33), it appears to have developed on a site which was formerly occupied by Salt Marsh. Succession was made possible, in all probability, by some physiographic process which resulted in the deposition of sand over the Salt Marsh vegetation and Salt Marsh peat.

34. *Salt Grass-Sea Myrtle Savanna* (BS)—The vegetation indicated by this class of mapping units is similar in appearance and composition to that described above (sect. #33). It differs in that the shrub stratum is more dense and more nearly continuous and *Juniperus virginiana* is either absent or present only as small individuals which do not exceed the *Baccharis halimifolia* in height.

35. *Fresh Marsh-Marsh Thicket Mixture* (MMt)—The vegetation of areas indicated by this mapping unit class usually consists of small, dense stands of Low Marsh Thicket which alternate with small, open areas of Fresh Marsh. The herb stratum, being absent or meagerly developed under the shrubs, is not continuous. The total shrub cover is estimated between 50% and 75%.

The composition of the vegetation cover in these areas is variable to the same extent as that of areas mapped as Fresh Marsh (sect. #4) or Low Marsh Thicket (sect. #13). The habitats occupied by these mixtures are of the same general character as those occupied by Fresh Marsh and Low Marsh Thicket communities.

36. *Dunegrass-Sea Myrtle-Marsh Thicket Mixture* (ABMt)—The vegetation cover of one unusual area (Fig. 2:2) is a jumbled mixture of species which are not commonly found in the same community. This vegetation occupies a low, broad, sand ridge parallel to the bay shoreline and separated from it by a narrow, sandy beach. The narrow beach provides a supply of sand and southwesterly winds provide the physical force necessary for transporting the sand onto the ridge. The ridge is higher on its western flank and lower on its eastern flank which is bordered by Brackish Marsh (see sect. #37). The microrelief on top of the ridge is quite irregular.

The herb stratum of this particular community includes *Ammophila breviligulata, Spartina patens, Hibiscus palustris*, and *Carex* spp. The shrub stra-

tum is composed chiefly of *Baccharis halimifolia*, but *Myrica pensylvanica*, *Smilax rotundifolia*, and *Rosa rugosa* are also present. This area is representative of many smaller areas whose vegetation could not be adequately classified by the methods employed in surveying and mapping. Most of these smaller areas of indeterminate character were too small to warrant separate mapping and were therefore included in other mapping units.

37. *Brackish Marsh-Marsh Thicket Mixture* (MSMt)—This mapping unit class designates one sizable area (Fig. 2:1-2) near the north end of the park. Ground water salinity in this area is generally less than 5 parts per thousand, but the herb stratum is virtually identical to that of a typical Salt Marsh. The surface is marked by a network of drainage ditches dug by the Civilian Conservation Corps in the mid-1930's. These ditches are now clogged, and the area does not drain freely into the bay. The sand ridge (sect. #36) along its western border is effective in preventing tidal flooding.

Only the occasional presence of *Hibiscus palustris*, *Rhus radicans*, and a few sedges gives any indication that the vegetation between the ditches is any different from that of typical Salt Marsh (sect. #6). The ditch banks, which are higher by a foot or so, are occupied by a variety of halophytic and hydrophytic species including *Iva frutescens* var. *oraria*, *Baccharis halimifolia*, *Rhus radicans*, and *Hibiscus palustris*. *Vaccinium corymbosum* extends into this area along ditch banks near its eastern boundary.

Why this area should remain virtually unchanged while other similar, but smaller, areas appear to have undergone considerable environmental and vegetational change is a question that cannot be answered on the basis of information presently available. Perhaps its large size has affected the rate of leaching necessary to reduce salinity, and its ground water salinity has only recently been reduced to a point low enough to allow the invasion of non-halophytic species.

38. *Brackish Marsh-Sea Myrtle Thicket Mixture* (MBt)—The areas indicated by this class of mapping units are presumed to have had a history similar to that of the area described above (sect. #37). These areas (Fig. 2:17-20 and 26-28) also appear to have been occupied, in former times, by typical Salt Marsh communities. They too were drained by ditches dug in the early 1930's, and they too are now separated from the bay and from tidal flooding by low, ice-formed sand ridges (sect. #3).

The habitats occupied by this mixture are virtually identical to those already described (sect. #5) for Brackish Marsh.

An analysis of 38 meter-square quadrats in an area judged to be representative of this kind of vegetation indicates an herb cover of 32% and a shrub cover of 75%. The herb cover is composed of *Spartina patens*, *Hibiscus palustris*, *Dryopteris thelypteris*, *Juncus canadensis*, and a few other species. The shrub stratum includes *Baccharis halimifolia*,

Rhus radicans, *Acer rubrum*, *Juniperus virginiana*, *Rosa rugosa*, and *Myrica pensylvanica* in that order of importance.

39. *Salt Grass-Marsh Elder Savanna* (IS)—The communities represented by this class of mapping units occur (Fig. 2:29-34) between areas of typical Salt Marsh (sect. #6) and areas of Salt Grass-Sea Myrtle-Red Cedar Savanna (sect. #33).

The general aspect of these communities (Fig. 7) is that of an open thicket about 4 to 5 ft high which overtops a dense grassland less than 1 ft high. An analysis of 58 meter-square quadrats on transect VI (Fig. 2:31) indicates a total herb cover of 96% composed entirely of *Spartina patens* and a total shrub cover of 24% composed entirely of *Iva frutescens* var. *oraria* (marsh elder).

The average elevation of the habitat is 2.5 ft above mean sea level, and the substratum is salt marsh peat about 30 in. thick. The ground water salinity, measured in August, is 8.6 parts per thousand at the eastern edge, 18.3 in the middle, and 23.0 at the western edge.

TRANSITIONAL THICKETS

The mapping unit classes in this group, like those in the preceding group, designate areas in which the vegetation displays attributes of structure, composition, or habitat which are intermediate between one or several more discrete community types or vegetation types. The use of "T" and "t" together in the symbol for a mapping unit signifies a dense thicket whose canopy is irregular—parts of it being below 7 ft and parts of it between 7 and 15 ft in height—or a narrow transition from Low to High Thicket.

40-42. *Transitional or Irregular Thickets* (Tt, Ttx, DTt)—"Tt" signifies an area in which there is a transition from Low to High Thicket or in which small areas of Low Thicket alternate with small areas of High Thicket. Most of the communities so designated occupy mesic habitats and are composed of species which are characteristic of Low Mesic Thicket (sect. #11) or High Mesic Thicket (sect. #18).

"Ttx" signifies vegetation of the same structural character as described above but occurring in xeric habitats and composed of species which are characteristic of Low Xeric Thicket (sect. #9) and High Xeric Thicket (sect. #16).

"DTt" signifies an area in which Low Dune Thicket (sect. #10) is transitional to High Dune Thicket (sect. #17) or the elements of these two kinds of communities are intimately mixed together. The characteristic habitats for this kind of vegetation cover are the foreslopes, tops, sides, and backslopes of secondary foredunes and transverse ridges.

WOODLANDS

The mapping unit classes in this group designate areas occupied by arborescent vegetation composed of trees over 15 ft in height which form a relatively uniform and continuous canopy whose total crown cover is over 50%. Shrubs, tree saplings, and lianas

form a dense growth, but not a discrete stratum, below the canopy.

43. *Red Cedar Woodland* (JW)—Red Cedar Woodland communities are junglelike masses of trees, shrubs, and lianas. The canopy (Fig. 13) is composed primarily of Red Cedar, and has an average height of 15-25 feet. The vegetation beneath the canopy is virtually impenetrable.

FIG. 13. View of Red Cedar Woodland facing northwest from 300m on transect II, note salt spray injury to Red Cedars (right side) at the seaward edge of the woodland.

An analysis of 60 meter-square quadrats laid out along a path cut through an area of less than average density shows a woody cover which, due to overlapping, totals 165%. Shrubs and trees below the canopy are so intimately intermingled and interlaced with lianas that they present a virtually solid wall of vegetation.

Canopy species were estimated to contribute in the following proportions to a total canopy cover of 132%: *Juniperus virginiana*—87%, *Ilex opaca*—20%, *Prunus serotina*—15%, *Amelanchier canadensis*—10%. Some of the *Juniperus* trees have a d.b.h. of 20 in., but most of the other trees are less than 8 in. d.b.h. Shrub cover was estimated as follows: *Rhus radicans*—12%, *Rosa virginiana*—10%, *Myrica pensylvanica*—6%, and *Vaccinium vacillans*—5%. The cover contributed by lianas—*Smilax rotundifolia, Rhus radicans,* and *Parthenocissus quinquefolia*—could not be estimated with accuracy because it was necessary to remove these plants in order to survey the transect and lay out the quadrats.

Species present in other parts of the Red Cedar Woodland include virtually all of those shrubs and trees previously listed in describing the various forms of xeric and mesic thicket (sect. #9, 10, 11, 12, 16, 17, 18, 19, 20).

The habitats occupied by Red Cedar Woodland are mostly between 5 and 10 ft above mean sea level and therefore range from mesic to xeric. All the areas mapped as Red Cedar Woodland (Fig. 2:3-7, 8, 11, 15, 18, etc.) are located at a distance of 300 m or more from the ocean shoreline. Substratum conditions are variable and so are the kinds of vegetation found at the periphery of such areas. The seaward sides of most Red Cedar Woodlands are bordered by Low Thickets and High Thickets which, because of salt spray pruning, form a distinct canopy angle that slopes upward towards the west. "Burned" foliage on the eastern (seaward) sides of these communities attests to the relatively high intensity of salt spray experienced at canopy height. At the interior, however, and on the western borders of Red Cedar Woodlands, there is rarely any evidence of salt spray damage.

The successional status and distributional pattern of this community type are reserved for further consideration in a later section. By inference from its structural and compositional characteristics, it appears to be a terminal or subterminal stage in converging lines of succession in the xerosere, hydrosere, and halosere.

44. *Pine Woodland* (PW)—Pine Woodland communities (Fig. 14) resemble Red Cedar Woodland communities only in respect to their arborescent structure. Pine Woodlands are restricted to a small area (Fig. 2:3) in the northwestern corner of the park.

FIG. 14. View of Pine Woodland facing west from 400m on transect I, note salt spray injury to tops of Pitch Pine in the foreground, stakes indicate line of transect to grove of Pitch Pine (*Pinus rigida*) and White Cedar (*Chamaecyparis thyoides*) in the background.

They have a fairly distinct, comparatively open canopy between 15 and 30 ft in height, and a well-developed and distinct shrub stratum occurs in some groves.

An analysis of 116 meter-square quadrats on transect I (Fig. 2:3) indicates a total canopy cover of 67% and a total shrub cover of 70%. The canopy is composed of *Pinus rigida* (pitch pine) 46%, *Chamaecyparis thyoides* 19%, and *Quercus marilandica* 2%. The shrub stratum is composed of *Vaccinium corymbosum* 36%, *Kalmia angustifolia* 26%, *Chamaecyparis thyoides* 5%, and traces of *Smilax rotundifolia, Quercus ilicifolia, Gaylussacia frondosa, Ilex glabra,* and *Myrica pensylvanica*. There is no herbaceous stratum, but a few moist depressions support clumps of Sphagnum moss and *Drosera rotundifolia*. In some groves (Fig. 14) Chamaecyparis and

shrubs are absent, and in a few, Chamaecyparis is more abundant than Pinus.

In other parts of the same general area (Fig. 2:2-4), there are scattered individuals of various other tree species. Some small groves are composed chiefly of *Ilex opaca, Quercus marilandica,* and *Quercus falcata.* (*Quercus falcata* is thought to reach the northern limits of its geographic distribution on Island Beach.) Also present but not abundant are scattered individuals, some over 10 in. d.b.h., of *Quercus alba* and *Quercus phellos.*

The average elevation of the two groves studied in detail (Transect I, Fig. 2:3) is 2.6 ft above mean sea level, and the water table lies at an average depth of 14 in. below the surface. The substratum is sand over coarse gravel of the kind found in the surf zone just off the ocean shoreline. Judging from the gnarled and burned appearance of some of the canopy trees, the incidence of salt spray at canopy height is sufficient to cause pruning of the taller trees.

These groves of Pine Woodland all occur in depressions surrounded by higher dunes which are occupied by Beach Heather communities and a scattering of *Juniperus virginiana, Quercus falcata, Q. ilicifolia,* and *Q. marilandica.* The presence of Pine Woodland in an area where Red Cedar Woodland is much more prevalent and apparently more characteristic cannot be readily explained, and its significance in uncertain.

45. *Red Cedar-Pine Woodland* (JPW)—The two small woodland communities indicated by this class of mapping units (Fig. 2: 3-4) are characterized by canopies composed equally of *Juniperus virginiana* and *Pinus rigida.* The vegetation below the canopy, however, is quite similar to that described for Red Cedar Woodland (sect. #43) in which there is no *Pinus rigida.*

46. *Swampy Red Cedar Woodland* (MJW)—The area (Fig. 2:5-6) mapped as Swampy Red Cedar Woodland differs from the rest of the Red Cedar Woodland in being generally more open, occurring on a hydric site, and in having an herb stratum. The herb stratum has a composition like that described for Brackish Marsh (sect. #5).

DISCUSSION

The foregoing description should provide ample evidence that the appelation of "vegetation-complex" to the vegetation of Island Beach is fully justified. The actual range of compositional variation, however, has not been explored for any of the vegetation mapping units described in the preceding pages. The methods employed in this general survey do not provide the kind of quantitative data required for a statistical treatment. If suitable data were available for analysis by the linear ordination technique described by Curtis & McIntosh (1951) or the multidimensional ordination technique described more recently by Bray & Curtis (1957), it could undoubtedly be demonstrated that many of these mapping unit classes (community types), especially Fresh Marsh

and Low Marsh Thicket, represent vegetational continua.

In spite of the floristic variation within certain mapping unit classes, the combination of structural, compositional, and environmental criteria makes it relatively easy to distinguish between adjacent mapping units. The magnitude of these differences justifies the consideration of individual mapping units (plant communities) as natural units of vegetation cover. Likewise, the similarity of structure, composition, and habitat exhibited among the individual mapping units of each class is sufficiently great to justify the consideration of each mapping unit class as a natural unit of vegetational composition (community type). The spatial arrangement of these units forms a complex vegetation pattern which conforms, presumably, to an environmental pattern of equal complexity and arrangement.

The vegetational patterns occurring on Island Beach are not unique, but they do display certain features which are not usually emphasized in descriptions of maritime vegetation. Boyce (1954), Davis (1957), and many others have described the vegetation of maritime strand as occurring in zones represented by three types of vegetation. According to Davis (1957), these are: "(1) a pioneer type composed mostly of herbaceous plants; (2) a scrub type of woody shrubs and vines and dwarf trees with a few associated herbs; and (3) a forest type dominated by trees." Oosting (1954) lists marsh as a fourth characteristic type of maritime vegetation. As a result of this common treatment, one may be left with the impression that these zones are more or less uniform in structure and composition. These same zones are often interpreted as stages in biotic (autogenic) succession from pioneer herbaceous communities to climax forests. The vegetation zones of Island Beach are obviously not uniform; and for various reasons to be explained later, they cannot be adequately interpreted as stages in biotic succession.

The shore zone is an important part of the topographic and environmental patterns which will be described later, and its boundaries are usually rather sharp, but it supports only a few annuals, e.g., *Cakile edentula,* and cannot be treated as a significant vegetation zone. The Dunegrass or herbaceous zone is the most sharply defined and most nearly uniform of the four vegetation zones which can be recognized on Island Beach. Its eastern boundary corresponds to the wave-cut notch (or nip) at the base of the primary foredune ridge which is parallel to the ocean shoreline. In some places, its western boundary grades into an herb-shrub zone; and in other places, it is marked by a sharp transition into consolidated thicket. In the northern half (Fig. 2:1-20) and at the southern tip (Fig. 2:35-41) of the study area, the scrub or shrubby zone is characterized by vegetation whose aspect is about equally divided between shrubby and herbaceous plants. The sector between these (Fig. 2:20-35) has a comparatively well-developed shrubby zone whose aspect is that of a very dense

thicket varying in height from 1 to 15 ft. The arborescent zone is best developed on a wider portion of the bar near the northern end of the park (Fig. 2:2-6), and disjunct stands of Red Cedar Woodland occur here and there but principally in the northern half of the park. The marsh zone, on the other hand, is best developed on a wider portion of the bar near the southern end of the park (Fig. 2:29-34), and relict areas of tidal-marsh (mapped as Brackish Marsh), which have been changed by physiographic and biotic processes, occur all along the bay shore but with greatest frequency in the southern half of the park (Fig. 2:20-41). The vegetational zones (and topographic zones with which they appear to coincide) are quite diversified and not at all uniform.

The vegetation of the herbaceous zone is composed almost entirely of communities belonging to the Dune-grass community type. The shrubby, arborescent, and marsh zones, on the other hand, are represented not by uniform types of vegetation cover but rather by mosaics of many plant communities which are quite different in structure and composition. The absence of trees is the chief distinguishing characteristic of the shrubby zone and the marshy zone.

Each zone of this zoned mosaic, and each of the communities included in it, is subject to "cornering" and/or "effusion" (*coincement* and *effusion*) as described by Dansereau (1956). Cornering refers to the narrowing and effusion to the broadening of vegetation zones and environmental gradients. On a regional scale, these phenomena are correlated with climatic differences which are controlled by geographic and orographic (locational) factors. On a local scale, as applies to an area the size of Island Beach, they are correlated with habitat differences and environmental gradients which are controlled largely by topographic, physiographic, and edaphic factors.

The working hypotheses to be considered in the remainder of this report can be summarized as follows: (1) The complex, zoned mosaic, vegetation patterns on Island Beach appear to conform closely to topographic patterns of a similar outline. Especially important are the elevation, configuration, and orientation of surface features (landforms and facets) and their relative distance from the ocean shoreline. (2) The general relationship between vegetational and topographic diversity is probably due to the influence of topography in controlling the intensity or amount of significant limiting factors in different habitats. (3) The principal limiting factors in the environmental complex of Island Beach appear to be those concerned with: sand movement, wind-borne salt spray, available soil moisture, and ground water salinity.

Before attempting to test these hypotheses, it is important to seek an answer to the question "What is the topographic pattern, and how was it formed?"

TOPOGRAPHY AND ENVIRONMENTAL PATTERNS

The second phase of this study is based on the premise that the zoned mosaic vegetation pattern of Island Beach can be explained, for the most part, in terms of cornering and effusion. This approach further assumes that vegetational diversity is closely associated with environmental diversity and that the vegetation pattern represents the present summation of plant responses to a corresponding environmental pattern. In attempting to describe this environmental pattern, topography has been given first consideration (as suggested by Oosting 1954) and is treated as a major habitat control (as suggested by Dansereau 1957). It has already been demonstrated that vegetation zones and topographic zones are roughly coextensive and that the habitats occupied by certain plant communities coincide exactly with the boundaries of particularly topographic facets.

Vegetation patterns have been described in terms of the structure, composition, and distribution of plant communities. Environmental patterns will now be described in terms of the environmental character and distribution of topographic facets. In this proposed analysis of environmental patterns, observational and analytical data are presented to show: (1) the influence of various physiographic processes on topographic patterns, (2) the distribution of plant communities and plant species in relation to topographic patterns, and (3) the influence of topographic patterns on limiting factor gradients. This is followed by an experimental study of the response of plant populations to one environmental factor gradient (salt spray).

PHYSIOGRAPHIC PROCESSES AND TOPOGRAPHIC PATTERNS

Without trying to set a particular sequence of cause and effect, it is possible to recognize interrelations between topography and vegetation on one hand and between topography and environmental gradients on another. Because it controls the intensity of limiting factors but does not influence plants directly, the topographic pattern occupies a central and diagnostic position in this attempt to analyze a complex environment. Because its interactions with other environmental factors are numerous and significant, topography can serve, in many ways, as a kind of index to total environment.

The total relief of Island Beach is slightly less than 40 ft, but the elevation, location, configuration, and arrangement of characteristic landforms are such that four relatively distinct topographic zones (see Table 2 and Fig. 19) are usually recognizable. The shore zone (about 50 m wide) and the zone of primary or active dunes (about 150 m wide) are easily distinguished. Together they comprise a diversified, 200 m wide strip which extends, almost without interruption, from the northern to the southern limits of the area studied. The zone of secondary or inactive dunes and the bayshore zone are less easily

distinguished. The bayshore zone is best developed in the southern sector of the bar (Fig. 2:30-34) where it is inter-tidal and composed of peat. The zone of secondary dunes, on the other hand, is best developed in the northern sector of the bar (Fig. 2:2-6) where it is well above high tide and is composed of sand over gravel. Elsewhere these two zones may be discontinuous and alternate, very narrow, or entirely absent from the topographic profile from east to west. Each of these four zones is characterized by differences in topography produced by differences in physiographic processes. Shore processes are largely independent of vegetation, but the physiographic processes responsible for the configuration of the primary (active) and secondary (inactive) dunes and the bayshore (marshy) zone require the interaction of physical forces (such as winds, waves, or tides) with biotic forces in the form of plant communities.

ORIGIN AND BEHAVIOR OF OFFSHORE BARS

Island Beach is part of an offshore bar or barrier beach of the type recognized by Johnson (1919) as characteristic of emergent or compound coastlines. A young coastline of emergence is a gently titled plain of unconsolidated, marine-deposited sediments newly exposed to the action of waves. Because the water for a long distance offshore is rather shallow, larger waves break farther from shore. The only waves to reach the newly emerged shoreline are small waves of translation.

Johnson postulates that storm waves breaking in deep water offshore cause the erosion of a shallow trough and the deposition of a low, submarine bar roughly parallel to the exposed shoreline. The elevation of this bar above sea level, by some process not described in the literature, results in the formation of an offshore bar which is parallel to the original shoreline but separated from it by a shallow lagoon.

The filling of the lagoon and the subsequent elimination of both the lagoon and the offshore bar are described by Johnson (1919), Knight (1934), and Miller & Egler (1950). Sediments are deposited in the lagoon by rivers and by tidal currents flowing through inlets. In its later stages, the filling process is augmented by submarine vegetation in moderately deep water and by tidal-marshes in shallow parts of the lagoon which are exposed at low tide.

Meanwhile, the active shoreline of the offshore bar is in a state of flux. At different times and in different parts, it may undergo either erosion or deposition. Oscillations in these processes result in a state of dynamic equilibrium; but under the influence of ocean winds and waves, especially during severe storms, the net movement of the shoreline and the offshore bar is ultimately landward. The terminal stage of this marine geomorphic cycle is reached when all traces of the offshore bar and the lagoon have been removed and the active shoreline coincides with the original shoreline of emergence.

Johnson (1919) describes topographic conditions in a few areas on the northeastern Atlantic coast of

the United States, but his major concern is with shore processes. Oosting (1954) presents a brief summary of topographic conditions along the southeastern Atlantic and Gulf coasts of the United States. The details of landward migration, however, and the attending processes of topographic change have not yet been described for any sizable stretch of coast in New Jersey or the adjacent states.

THE SHORE ZONE AND SHORE PROCESSES

The action of waves on an exposed shoreline is such that onshore and offshore processes operate simultaneously. Whenever these processes are in equilibrium, as they appear to be at Island Beach, the shore profile is relatively stable and is referred to (Johnson 1919) as a *profile of equilibrium*. Profiles of equilibrium may exhibit a wide range of topographic configurations; but, regardless of configuration, they represent a momentary balance between the power of waves and the resistance of the beach. Since the power of waves is proportional to their height, and the highest waves accompany storms, the greatest amount of both erosion and deposition occurs during storm periods.

Under normal conditions of tide and wave activity, the shore zone of Island Beach (Fig. 15) can be subdivided into foreshore and backshore. The litter line which marks the highest recent tide and the nip or wave-cut notch (cut by storm waves) provide convenient boundary lines.
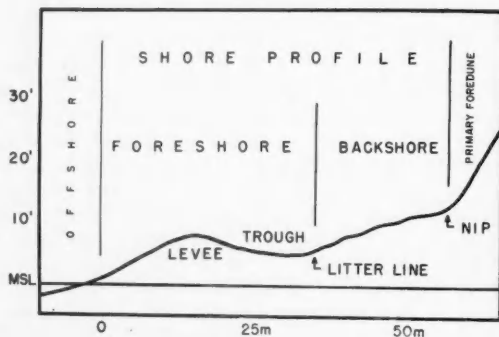
FIG. 15. Typical configuration of the shore profile at Island Beach, New Jersey.

During periods of comparative equilibrium, sand is moved across the shore zone in the following manner: The swash of breaking waves deposits sand on the levee near the center of the foreshore. Occasional waves wash over the levee and carry some sand into the trough. From the foreshore, sand may be carried to the backshore by high tides or occasional high waves, but this is usually accomplished by wind. The backshore, being above high tide most of the time, serves as a reservoir from which sand is removed by wind and deposited farther inland. Most of the sand removed from the backshore by wind is deposited as a blanket on the primary foredunes adjacent to the shore. Some sand is carried through wind-

blown or wave-cut channels and deposited farther inland in the primary backdune area.

PRIMARY AND SECONDARY DUNE PATTERNS

The landforms which characterize the primary and secondary dune zones are: dunes, hollows, dune ridges, swales, channels, and sandy flats. A *dune* is simply a windblown pile of sand. A hollow is either a low place between irregular dunes or a depression surrounded by higher ground. A *dune ridge* is a straight row of dunes, and *swale* refers to the trough between parallel primary and secondary dune ridges. *Channel* refers to blowouts or wave-cut channels which interrupt dune ridges and cut across backdune areas. *Sandy flats* are broad, low, generally level areas lying between primary and secondary foredunes or west of secondary foredunes at a distance of more than 200 m from the ocean shoreline.

Variations in the topographic configuration of the different dune zones, as shown by contrasting east-west transects, will be described in a later section (page 29). It is sufficient at this point to note that the magnitude of topographic diversity is roughly equivalent to the magnitude of vegetational diversity indicated by the vegetation map.

The primary foredune ridge is a straight and nearly continuous line of dunes immediately parallel to the shore. Broken by channels which vary in frequency from one place to another, it tends to be low (10-20 ft) in areas where the bar is wide and high (20-35 ft) in areas where the bar is narrow. The primary backdune area varies from a high sandy flat (Fig. 2:2-6) to a conglomeration of dunes and hollows (Fig. 2:10-12) to a broad, low swale between parallel foredune ridges (Fig. 2:28-29).

The secondary foredune ridge is a straight but discontinuous line of wide-spaced, lower, more stable, and apparently much older dunes centered on a line about 200 m from the ocean shoreline. The longest continuous segment of secondary foredune ridge (Fig. 2:28-30) ranges from 20-25 ft elevation above mean sea level, is relatively broad, well-stabilized, and has gentle eastern (seaward) and western (landward) slopes. The secondary backdune area varies from a broad, low, sandy flat underlain by peat (Fig. 2:29-33) to a high, broad area of dunes and hollows (Fig. 2:3-5) underlain by coarse sand and gravel. In the former area it borders on a peaty bayshore, and in the latter it extends to a narrow, sandy bayshore.

The boundary between primary or active dunes and secondary or inactive dunes corresponds to a line connecting points which represent either the eastern bases of secondary foredunes, or, in areas (Fig. 17, profiles II & IV) where secondary foredunes and primary backdune areas are not recognizable, the western bases of primary foredunes. For all practical purposes, this is a straight line parallel to and 200 m west of the ocean shoreline.

The zone of primary dunes is characterized by relative instability and a continuing history of frequent and rapid change. The zone of secondary dunes, on the other hand, is relatively stable and has had a history, as evidenced by the vegetation, of less frequent and slower change. Physiographic processes in the former are frequently dominated by physical forces which promote change. In the latter, they are usually dominated by biotic forces which resist change.

DUNE-BUILDING PROCESSES AND PRIMARY DUNES

The prerequisites for the building and shaping of dune topography are: (1) a source of sand, (2) a means of transporting it from one place to another, and (3) a means of holding it in place after deposition. At Island Beach, the chief source of sand is the shore, and this supply is constantly renewed by wave action. Wind is the principal force responsible for the transportation of sand from the shore to dunes. Vegetation, by reducing wind velocity at the surface, causes the sand to be deposited and reduces the probability of its subsequent removal. Waves become periodically important only during severe storms.

Prevailing winds in the latitude of Island Beach are westerly; but, because they do not blow over loose sand, they are not effective in dune-building. Sea breezes may account for some movement of sand, but the strongest, most frequent, and therefore most effective easterly winds are those which accompany northeasterly storms. Such storms may occur at any time during the year, but they are especially common in the spring and fall. The importance of northeasterly winds in transporting sand is evidenced by the orientation of most blowouts and channeled deposits in a northeasterly by southwesterly direction.

The zone of most active dune-building appears to be coextensive with the herbaceous or Dunegrass vegetation zone. This zone is widest and apparently most active in the northern end of the park (Fig. 2:1-6). In 1932, a road was built along the landward base of the primary foredune ridge along this stretch. Most of this road is now covered by windblown sand which continues to spill over the low (15 ft) dune ridge. Uniform in height and scarcely broken by blowouts, this low primary foredune ridge appears to be building upwards at a rapid rate.

The Dunegrass zone of this area is divisible into two sub-zones: an outer (seaward) zone in which *Ammophila breviligulata* is consolidated into a vigorous and nearly continuous community and an inner (landward) zone in which it is degenerate and represented only by a few depauperate clumps. Numerous dead tufts testify to a former more vigorous condition of Ammophila in the inner zone.

Methods—To study the interrelations between Ammophila and the primary dune-building process, two east-west (*i* and *ii*) and three north-south (*iii*) transects were established in the area described in the two preceding paragraphs (Fig. 2:1-6). The east-west transects begin at the base of the primary foredune ridge and extend inland to the first contact with Low Thicket. The north-south transects are 20 m apart and lie parallel to the eastern (seaward) edge

of the Dune grass zone. The first is 20 m inland from the edge and lies entirely within a vigorous stand of Ammophila having a total cover of 15%. The second, 20 m west of the first, is in the transition from vigorous to degenerate Ammophila and has a vegetation cover of 5%. The third, 20 m west of the second, lies in an area devoid of living Ammophila except for a few clumps. *Solidago sempervirens* and *Euphorbia polygonifolia* are present and relatively abundant, but the total vegetation cover is less than 1%.

Each transect was marked by wooden stakes placed at 10 m intervals. Notches were cut near the top of each stake. Then, using the notches as guides, a heavy twine was stretched taut between successive stakes. The distance from the taut string to the surface of the sand was then measured in centimeters at 1 m intervals, and the results were averaged by 10 m increments. On the first day (Sept. 23, 1956), a series of three measurements was made. A comparison of the results indicated an average measurement error of less than 0.5 cm. Measurements were repeated at intervals through the following winter and again the following September. The differences between successive measurements were averaged by 10 m increments and expressed in centimeters as net deposition or deflation of sand.

Results—Data obtained in this manner from the two east-west transects are shown in Table 5. Each column shows net deposition or deflation since the previous measurement. For example, the considerable deposition indicated (column headed 10/19) along both east-west transects took place between Sept. 23 and Oct. 19, 1956. Most of this deposition probably occurred during a single northeasterly storm on Oct. 11 and 12. Another severe northeaster with winds of full gale force occurred the following year (1957) on Oct. 5, 6, and 7. This storm brought the study to a premature end because many of the wooden stakes, weakened by a year of exposure to the elements, were snapped off at ground level by the force of the wind.

The five series of measurements made between Sept. 1956 and sept. 1957 indicate a considerable amount of variation in deposition and deflation taking place along different parts of the two transects. The totals indicate more deposition than deflation in the eastern 60-m segments of both transects. The amount of deposition decreases sharply with increasing distance from the seaward edge of the Dunegrass community. The mutual relationship between deposition and Dunegrass (*Ammophila breviligulata*) and Japanese sedge (*Carex kobomugi*) seems obvious. The average net deposition of sand for 1 yr in the vigorous Dunegrass zone of the northern transect (i:1-40m) was about 17cm; and, on comparable parts of the southern transect (ii: 1-40m), 28cm. In the transition zone represented by sparse Dunegrass on the northern transect (i:41-60m) and by a mixture of Dunegrass and Japanese sedge on the southern transect (ii:41-60m) the average net deposition for the same period of time was about 3.3 and 5.1 cm, re-

TABLE 5. Deposition (+) and deflation (−) in cm. of sand along east-west transects across the primary foredune. The first measurement was made on September 23, 1956 and the last on September 28, 1957. Distance (D) is measured in meters west of the nip that marks the beginning of the primary foredune.

Transect i (See Fig. 2:3.3)

Vegetation	D	10/19	11/16	12/19	2/9	9/28	Total
VIGOROUS DUNE-GRASS COMMUNITY	1– 10	+14.5	+ 8.1	+ 8.4	−12.4	+15.2	+33.8
	11– 20	+ 7.9	− 0.2	+ 2.0	+ 0.8	+ 9.6	+20.1
	21– 30	+ 1.6	+ 1.9	+ 0.4	+ 2.7	+ 1.5	+ 8.1
	31– 40	+ 2.2	+ 2.1	+ 0.8	+ 0.9	+ 1.0	+ 7.0
SPARSE DUNEGRASS	41– 50	+ 0.9	+ 0.3	+ 0.1	+ 2.1	+ 0.4	+ 3.8
	51– 60	− 2.8	+ 5.2	+ 4.1	− 4.1	+ 0.3	+ 2.7
DEGENERATE DUNE-GRASS & BARE SAND	61– 70	+ 0.1	+ 2.4	+ 1.3	0.0	− 4.0	− 0.2
	71– 80	+ 0.8	− 0.8	0.0	+ 2.2	− 6.3	− 4.1
	81– 90	+ 1.0	+ 2.0	+ 0.3	− 0.8	− 2.5	0.0
BEACH HEATHER COMMUNITY	91–100	+ 2.7	+ 0.7	+ 0.6	− 0.4	− 1.5	+ 2.1
	101–110	+ 0.8	− 0.3	0.0	+ 1.4	− 0.6	+ 1.1

Transect ii (See Fig. 2:4.1)

Vegetation	D	10/19	11/16	12/19	2/9	9/28	Total
VIGOROUS DUNE-GRASS COMMUNITY	1– 10	+35.7	− 2.1	+ 8.6	+ 1.5	+ 9.5	+53.2
	11– 20	+ 2.7	+16.2	− 7.2	+ 8.4	+ 9.0	+29.1
	21– 30	+ 6.2	+ 9.0	+ 1.7	+ 1.2	+ 2.7	+20.8
	31– 40	+ 3.7	+ 0.3	+ 1.3	+ 0.5	+ 3.0	+ 8.8
DUNEGRASS & JAPA-NESE SEDGE	41– 50	+ 1.5	+ 2.8	+ 1.8	+ 1.7	+ 0.4	+ 8.2
	51– 60	+ 0.9	− 2.3	+ 2.8	+ 0.9	− 0.3	+ 2.0
DEGENERATE DUNE-GRASS & BARE SAND	61– 70	+ 0.5	− 0.1	+ 1.1	+ 1.8	− 3.7	− 0.4
	71– 80	+ 0.1	+ 0.3	− 0.3	+ 0.6	− 1.9	− 1.2
	81– 90	+ 0.7	0.0	+ 1.4	+ 0.6	− 2.3	+ 0.4
	91–100	+ 2.0	− 3.9	+ 3.9	+ 1.5	− 3.3	+ 0.2

spectively. In the degenerate Dunegrass zone (i:61-90m) and (ii:61-100m), deflation exceeds deposition by a small amount. The area immediately to the east of Low Thicket (i:91-110m), Beach Heather, and (ii:81-100m) bare sand is an area in which deposition exceeds deflation by a small amount.

The Japanese sedge traversed by the southern transect (ii:42-57m) forms a much lower (about 15cm) and much more dense vegetation cover (80% total cover) than does Dunegrass. A separate analysis of measurements made in this colony indicates an accumulation of 8.9 cm of sand on the seaward half and 3.4 cm on the landward half of the colony. In April 1958, the whole colony was observed to be partially buried by sand.

Table 6 shows the deposition and deflation along three north-south transects. Again the variation and fluctuation at any one place is obvious, but the net result for the year is an average accumulation of 15.7 cm. of sand in the vigorous Dunegrass community and 1.8 cm in the transition from vigorous to degenerate Dunegrass. In the degenerate Dunegrass zone, there is a certain amount of deposition and deflation but to no significant net change.

An accumulation of sand was noted along the seaward edges of Low Thicket bordering the degenerate Dunegrass zone in this general area and at the

TABLE 6. Deposition (+) and deflation (−) in centimeters of sand along north-south transects on the primary foredune at 20, 40, and 60 m west of the nip that marks the beginning of the primary foredune. The first measurement was made on September 23, 1956 and the last on September 28, 1957. Distance (D) is measured in meters from north to south.

Transect iii (See Fig. 2:4.2)

Vegetation	D	10/19	11/16	12/19	2/9	9/28	Total
20 meters	1–10	+ 3.9	+ 3.9	+ 3.6	+ 3.7	+ 0.7	+15.8
VIGOROUS DUNE-	11–20	+ 5.3	0.0	+ 1.7	+ 0.8	+ 0.6	+ 3.4
GRASS	21–30	+19.2	− 1.0	+ 3.5	+ 1.2	− 3.0	+19.9
	31–40	+10.8	+ 5.5	+ 0.2	− 0.3	+ 2.6	+18.8
AVERAGE FOR THE YEAR:							+15.7
40 meters	1–10	+ 0.4	+ 4.8	+ 1.1	+ 1.2	− 0.1	+ 7.4
TRANSITION	11–20	+16.7	−16.8	+ 1.8	− 0.5	− 0.5	+ 0.7
	21–30	+ 0.7	+ 0.3	+ 1.4	+ 1.1	− 3.0	+ 0.5
	31–40	− 0.4	+ 2.4	− 0.1	− 0.8	− 2.4	− 1.3
AVERAGE FOR THE YEAR:							+ 1.8
60 meters	1–10	+ 0.9	+ 1.9	+ 0.3	− 0.7	− 1.7	+ 0.7
DEGENERATE DUNE-	11–20	+ 0.6	+ 2.5	0.0	− 0.6	− 2.7	− 0.2
GRASS	21–30	+ 0.4	+ 1.7	+ 0.8	+ 0.5	− 2.1	+ 1.3
	31–40	− 0.8	+ 0.6	+ 1.1	+ 0.6	− 2.8	− 1.3
AVERAGE FOR THE YEAR:							+ 0.1

western ends of the two east-west transects. There was, however, no satisfactory way to adapt this method for use in dense thicket. Future studies could be made, perhaps, by using long, metal stakes that reach above the thicket canopy.

Discussion—The results of this study clearly establish the existence of a reciprocal relation between Dunegrass and sand deposition. This relationship, however, is not a simple matter of cause and effect. Persistent winds can transport sand and cause its accumulation in the form of a dune without the intervention of Dunegrass while Dunegrass can and does persist on mesic sites (Fig. 11) where the annual accumulation of sand is negligible.

An annual accumulation of sand appears to be necessary, however, for the survival of Dunegrass on xeric sites. The arguments in favor of this conclusion are: (1) It is vigorous and grows actively on xeric sites where deposition exceeds deflation by 7 cm or more per year. (2) It is less vigorous, depauperate, or dead on xeric sites where the difference between deposition and deflation is negligible. (3) It occurs in dense stands on mesic sites where deposition and deflation are nil and the surface is less than 2 ft from the water table.

On Island Beach, the Dunegrass community and the primary foredune ridge grow up together by a process which results from the interaction between physical forces (waves and wind) and biotic forces (plant communities). Waves replenish the shore's supply of sand, wind transports the sand inland, and Dunegrass causes the sand to be deposited and held in a particular pattern. Being built up of successive layers of sand which are thicker on the eastern side and thinner on the western side, these dunes have steep seaward (windward) slopes and gentle landward (leeward) slopes. This difference is augmented by storm wave erosion. (Dunes built entirely by wind, e.g., desert dunes, tend to have long, gentle windward slopes and steep leeward slopes.) From the standpoint of physiographic process, the cause of dune-building is to be found in the complex interactions of waves, wind, and vegetation.

BLOWOUT PROCESSES AND CYCLES

As indicated by the vegetation map (note breaks in dune ridge line), the primary foredune ridge is broken by numerous channels of various sizes. These channels, which are cut by wind or by waves, become "pipelines" through which sand may be transported by easterly winds and deposited in the primary backdune area. Such channels are characteristic but apparently transient features of the Island Beach landscape.

Many blowout channels are associated with footpaths which lead from the main highway to the shore, but there is some question as to which came first—the blowouts or the footpaths. There can be no doubt that heavy pedestrian traffic along a path can contribute to the development of a blowout. Under ordinary dune-building conditions, the older rhizomes of Ammophila are protected by a layer of sand several inches in depth; but new rhizomes, produced early in the growing season when the deposition of sand is at a minimum, are closer to the surface, structurally more tender, and undoubtedly more susceptible to trampling injury. Continued use of the same path can kill the stabilizing vegetation, wear down the seaward slope of the foredune, and open a channel for the wind. Excessive deflation can then uncover more rhizomes thus widening and lengthening the gap until the ridge is breached by a blowout channel.

Disturbance, however, is not a prerequisite for the formation of a channel. High waves or strong winds or both, especially during severe storms, can open new channels or close old ones. Many of the larger channels are cluttered with heavy timbers and other debris washed there by storm waves. Other channels contain similar debris which is buried under wind-blown sand.

Sand carried through these channels is generally deposited some 50 to 150 m farther inland. Both the channels and the dunes deposited at their inland ends are oriented in a northeast by southwest direction, and the dunes have gentle eastern and steep western slopes. Subsequent stabilization, shifting by wind, and the slower alterations brought on by gravity and rain eventually change this initial form to that of a low, flat cone.

Channels do not remain open indefinitely. Many are now being closed by means of drift fences. Many others are being or have been closed by natural processes. Small, shallow channels are often closed during the growing season following their initiation.

Older channels, which are wider and deeper, often contain "haystack dunes" which are remnants of the former dune ridge whose backslope had been stabilized by shrubs before the blowout developed. After the steep slopes of the channel have been made gentle by wind and gravity, Ammophila can reinvade the sides. It also invades the flat floors of wider channels, and low dunes are built up on the floor. As the invading Ammophila becomes consolidated into a continuous community, the primary dune-building process may proceed to close the gap and fill the channel.

Being presently based only on observational data, the recognition of this cycle is tentative. The initiation, development, and repair of blowouts appear to occur, at least sometimes, as a cyclic process. The position of the shoreline and that of the primary foredune ridge appears to be stable or relatively stationary for periods of time sufficient to allow the completion of several cycles of dune-building, channel development, and repair. Apparently of great significance in the construction and alteration of topographic zones and in the landward migration of offshore bars, the behavior of such channels deserves a more intensive, long-term study.

The constructive processes of dune-building and blowout repair and the destructive processes of blowout initiation and development appear to operate simultaneously but not uniformly. Dune-building results in the formation of a primary foredune ridge and represents an interaction between physical forces and biotic forces in which the physical forces are strongly modified. The initiation and development of a blowout channel reflects the temporary ascendancy of physical forces over biotic. The irregular pattern of dunes and hollows in many primary backdune areas is thought to represent the deposits left at the ends of blowout channels which have been repaired. The systematic repair and disappearance of blowout channels represents the re-establishment of biotic influences. In the zone of secondary dunes, where the topography is essentially stabilized by vegetation, these processes operate much more slowly. Rapid changes in topography at a distance of more than 200 m from the ocean shoreline are brought about only by tidal waves and strong winds during severe storms.

DUNE-BUILDING PROCESSES AND SECONDARY DUNES

While the zone of secondary or inactive dunes is essentially a zone of stable topography, it is characterized by dunes which do not appear to have been formed by any process which can be observed in operation at the present time.

The secondary foredune ridge, briefly described in an earlier section, is composed of a row of wide-spaced, relatively stable, apparently old dunes of intermediate but conspicuous height. A typical secondary foredune (transect VI, Fig. 17) is moderately high (20 ft), relatively flat on top, and has about the same degree of slope east and west. The lower part of the seaward slope is usually occupied by a

Beach Heather community while the upper part is often bare. The top usually supports a low Dune Thicket, while the landward slope is commonly held in place by a High Dune Thicket dominated by *Prunus serotina* (Fig. 9). Some of these trees have sizable stems (6-10 in. d.b.h.) which attest to the considerable age and stability of the dunes they occupy.

The manner in which secondary foredunes are formed has not been determined, but several possibilities deserve consideration. (1) They may have been built up from sand carried through blowout channels in the primary foredune ridge. This suggestion is tentatively rejected for two reasons. Secondary foredunes are frequently higher than dunes in the primary backdune area which are known to have been formed in this manner, and present-day blowout activity does not appear to result in the transportation of sand over the required distance (200-250 m). (2) If it is postulated that Island Beach is a prograding bar, secondary foredunes can be interpreted as the remnants of an earlier primary foredune ridge. This theory has some advantages. It falls into line with the interpretation of maritime vegetation zones as seral stages in biotic succession. It also helps to explain the width of the bar which, in some places, is more than twice the distance of effective sand transportation under present conditions. The idea of a prograding bar is inconsistent, however, with the idea of landward migration and cannot be supported by evidence. Landward migration, on the other hand, is indicated by such evidence as the exposure of old peat deposits on the ocean shore at low tide and by the presence of a thin layer of sand covering more recent peat deposits along the bay shore. (3) Waves of hurricane magnitude are known to sweep across the bar from time to time. Undoubtedly these waves can and do carry large quantities of sand, and they are capable of cutting channels across dune ridges. It is difficult to conceive how such waves could possibly build secondary foredunes. (4) The theory which seems to be most consistent with the known facts is that secondary foredunes are the remnants of an old ridge which was formed by the primary dune-building process at a stage of development in which the intervening area between the shore and the secondary foredune was less well stabilized by vegetation than it is at the present time. There are several lines of circumstantial evidence and a few credible arguments in favor of this theory.

The extreme southern tip of Island Beach (Fig. 2:36-41) is known to be relatively young. The Southernmost mile of this stretch was formed during the last one hundred years by the southward migration of Barnegat Inlet (Lucke 1934). While much of this area has been badly disturbed by a long period of human occupancy and by recent (1954) dredging operations, a relatively undisturbed part of it (Fig. 2:36-37) still provides some clues as to the possible mechanisms of secondary foredune formation.

In this area, the primary foredune ridge is represented only by a series of low, disconnected dunes each of which is held in place by a colony of Ammophila. To all appearances, these small, isolated dunes are slowly becoming consolidated into a single ridge along a line determined by high tides and storm waves. A broad zone west of this incipient ridge is virtually devoid of vegetation, and the wind moves sand across it unimpeded. Scattered Ammophila grades into a Phragmites zone which is bordered on the west by Salt Marsh.

What might actually happen under natural conditions is obscured by an artificial dune composed of dredge materials, held in place by drift fence (Fig. 2:37-41). With a wide sweep for the wind across loose sand, it might be possible for the primary dune-building processes to operate first at a greater distance from the shoreline and later at the line of Ammophila consolidation along the edge of the shore. The farther line of deposition might be established at a boundary between sparse and denser vegetation.

One area in particular (Fig. 2:28-30), lends itself very nicely to this interpretation. The shore zone along this stretch is more or less typical. The primary foredune ridge is virtually continuous, uniform in height (20-25 ft), and rather narrow. The primary backdune area is a broad, trough-like swale. The secondary foredune ridge is lower and broader than the primary, and it is broken by several deep channels. The area west of the secondary ridge is a conglomeration of low dunes, hollows, and marshes.

The probable developmental history of this area has been hypothetically reconstructed and diagrammed in Fig. 16. As a young area (Fig. 16A), its configuration was similar to that of the relatively young, relatively undisturbed area (Fig. 2:36-37) mentioned in the third paragraph above. Having a wide sweep across unstable sand, the wind carried sand farther from the shore than is normally possible under present conditions. A straight line of deposition was established (Fig. 16B) by some means. It could have been established (as illustrated) along the edge of a consolidated thicket zone such as now borders tidal-marsh in other areas (Fig. 2:32). The consolidation of Dunegrass communities proceeded rapidly along this established line of deposition (Fig. 16B). The secondary ridge was then built up (Fig. 16C) by the same dune-building process as described earlier. The removal of sand from the intervening area (Fig. 16C) brought the surface nearer to the water table and thus provided more mesic conditions which favored the spread of Ammophila even without the regular accumulation of sand. As this broad Dunegrass zone (Fig. 16D) became consolidated along a line determined by high tides and storm waves, the maximum point of deposition was shifted to the east. The primary foredune ridge was built up (Fig. 16E) along the new line of deposition. Sand spilling over the ridge raised the surface of the primary backdune swale causing it to become more xeric.

PROFILE DEVELOPMENT
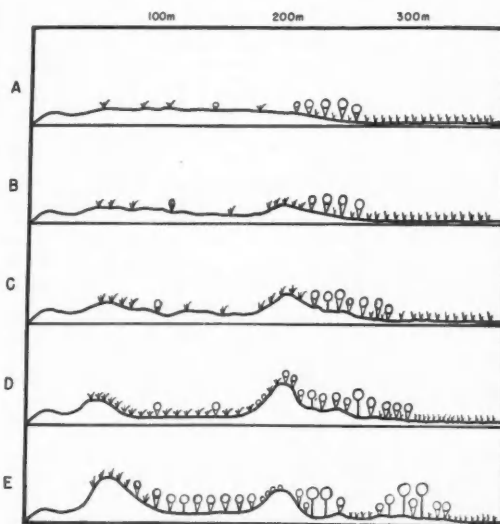
FIG. 16. Hypothetically reconstructed developmental history of secondary and primary dunes on a young part of an offshore bar. A-E, early to late stages.

Salt spray intensity was reduced by the intervention of the primary foredune ridge, and this area then became available for the establishment of a thicket. At the same time, the Dunegrass on the secondary foredune ridge was replaced by species which do not require a continuing accumulation of sand. The present irregularities in the topographic pattern were probably produced, during this period of changing environment and stabilization, by oscillations in the magnitude of physical and biotic forces which interact to control the physiographic processes involved.

EFFECTS OF INLETS AND STORM WAVES

Lucke (1934) made a rather thorough study of Barnegat Inlet and it developmental history. In a general theory, he proposed that inlets in offshore bars are opened by storm waves, maintained by tidal currents, and closed by sediments supplied by longshore currents. Longshore currents on the bay side of the bar move towards the inlet at ebb tide and away from the inlet at rising tide. Longshore currents on the ocean side move from north to south as a result of the onshore-offshore motion of waves approaching at an angle, predominantly from the northeast.

According to Lucke's theory, an inlet such as Barnegat Inlet migrates southward because the ebb and flow of tidal currents causes an excess of erosion on the south side and an excess of deposition on the north side of the channel. This migration is initiated by a simultaneous increase in the volume and velocity of tidal currents through the inlet and in the

amount of sediment delivered at the inlet by long-shore currents on the ocean side of the bar. In the case of Barnegat Inlet, both effects were accomplished by the closing of former inlets between Barnegat and the headland (Fig. 1) at Point Pleasant. Old charts show, for example, that Cranberry Inlet, located about 12 mi. north of Barnegat's present position, was opened during a storm in 1750 and closed during another storm in 1812. Eighteen inlets between Barnegat and the headland have become extinct, according to Lucke, in historical times. Accurate charts of the past century show that Barnegat Inlet has migrated southward in historical times at a rate of 1 mi. per 100 yrs.

Noticeable changes have occurred in recent years. The southern tip of the bar has been extended southward and widened somewhat since the aerial photographs used in making the vegetation map were taken in 1954. The two larger ponds indicated by the map (Fig. 2:40-41) have been filled in, and other minor changes in outline have occurred.

The north shore of the inlet is more or less crescent shaped, and it is bordered by a row of active dunes which are oriented northwest by southeast, roughly at right angles to the prevailing southwesterly winds. If the rate of southward migration were sudenly increased, these dunes would probably remain behind, in the same position they now occupy, to be reduced in height or stabilized perhaps by woody vegetation. The area immediately north of the inlet (Fig. 2:35-41) is half again as wide as shown by the vegetation map. It has been built up from sediments supplied by longshore and tidal currents. Salt Marshes in this area are underlain by peat which is no more than one foot deep as compared to two feet or more under marshes farther north (Fig. 2:31-32).

The pre-migratory position of Barnegat Inlet is difficult to ascertain for, in all probability, it has been migrating for a much longer period of time than can be documented. The area between Fig. 2:33 and 35 is a logical choice for the following reasons: this narrow section of the bar is parallel to a deep trough, perhaps a former inlet channel, in the bay. Also, in this area, there is a low transverse dune (Fig. 2:33, DTt) of the kind and shape that might be left behind by a migrating inlet or by the closure of an inlet which was much less active than Barnegat now is. The wide section of the bar immediately north of this position (Fig. 2:29-33) could have been built up in part by inlet-deposited sediments and in part by the marsh-building processes which accompany the establishment of tidal-marshes. Another area of similar width and shape but different topography and vegetation (Fig. 2:2-6) could have been formed in much the same manner at a much earlier time.

Transverse channels (Fig. 2:9, M,Mt, etc.) which match with large blowout channels in the primary foredune ridge are probably due to the action of storm waves. Several narrow sections (Fig. 2:16,

35-36) have been reported by eye-witnesses to be completely awash during hurricanes. Still other transverse features (Fig. 2:25-28) cannot be explained in such simple terms. The deep, narrow channels (M, Mt, Pond) which pass between transverse dunes (DTt) of peculiar shape and end in deltoid deposits (BJS) at Fig. 2:27 are suggestive of wave action, but neither the dunes nor the channels extend across the eastern half of the bar. This configuration may have been produced by storm waves which preceded the formation of the present pattern of primary and secondary foredunes.

BAYSHORE PROCESSES

The physiographic processes which operate on the bayshore zone of Island Beach are generally more localized, more diversified, and less intense than those operating on other zones.

The wider portions of the bar (e. g., Fig. 2:2-5, 29-34) have probably been built up by processes of longshore and inlet deposition augmented by marsh-building. Such areas are subsequently altered by the landward migration of dunes and dune topography while the position of the bar remains relatively stationary.

Tidal-marshes can presumably get established (Knight 1934) wherever the floor of the bay becomes sufficiently raised to be exposed at low tide. Once established in a quiet cove or over a larger shallow area, the Salt Marsh community bears the same general relation to tides and tideborne sediments as does the Dunegrass community to winds and windborne sand. Some of the sediments carried by tidal currents are deposited around the culms of *Spartina alterniflora* or *S. patens*. The combination of dead rhizomes culms, and sediments which comprise the peat of a tidal-marsh are gradually accumulated by this process. Marsh-building is much slower and more limited in its potential than dune-building, but both processes result from the interaction of biotic and physical forces.

Tidal-marshes may be removed from the influence of tides by another process, already described, which also requires the participation of physical forces (the mechanical action of ice moved by wind) and biotic forces (the growth of Reedgrass communities). Sand ridges stabilized by Reedgrass become more or less permanent. If the margin of a tidal Salt Marsh is circumscribed by such a ridge, the marsh is effectively removed from the effects of tidal flooding. Its vegetation and environment may then undergo radical changes.

The southwesterly winds which control wave action at the bay shoreline are less strong and have a much shorter fetch than the northeasterly winds which control wave action at the ocean shoreline. Wave action on the bay shore is therefore much milder than wave action on the ocean shcre. In some places, the bay shoreline is prograding by the deposition of sand and eelgrass (*Zostera marina*), and in other places

(Fig. 2:5-7), it is being eroded away as shown by the undercutting of trees and shrubs.

Along one considerable stretch (Fig. 2:1-7), there is a narrow, sandy beach. The amount and rate of dune-building made possible is commensurate with the supply of sand and the strength of the westerly winds which are available to transport it inland.

SUMMARY

The topographic pattern of Island Beach is a zoned mosaic similar in many respects, both general and particular, to the vegetation pattern. Shore processes which determine the configuration of the shore zone are entirely under the control of wind and waves. The configuration and pattern of inland zones designated as the primary and secondary foredunes and backdunes and the bayshore are determined by physiographic processes which result from the interaction of physical forces (wind, waves, and tides) and biotic forces (the growth of various plant communities). The zoned mosaic pattern of topography is a result of oscillations in the dynamic equilibrium obtained between the physical forces and biotic forces which operate differently in each zone and in different parts of the same zone. The east-west orientation of topographic zones, which extend north-south or parallel to the shoreline, is in line with the east-west orientation of winds, waves, and tides.

TOPOGRAPHY AND THE DISTRIBUTION OF PLANT COMMUNITIES

In the first part of this report, the vegetation pattern of Island Beach was described as a zoned mosaic. In the foregoing consideration of physiographic processes, the topographic pattern was described as a similar kind of zoned mosaic which is shaped by the operation of physiographic processes. The purpose of the transect studies described in the following pages is to provide quantitative bases for judging the closeness of association between vegetational and topographic patterns.

METHODS

The topographic profile was measured and the vegetation sampled along four contrasting transects (Fig. 2: I, II, IV, VI) by the following methods.

The transects were laid out by means of a transit theodolite along compass lines perpendicular to the main highway. The main highway lies, for most of its length, on a line which is 4° east of true north. Transects I, II, and IV run almost due east by west, and transect VI runs northeast by southwest. With the exception of number II, each transect extends from the ocean shoreline to the bay shoreline.

A path was cleared through the denser vegetation traversed by each transect, and wooden stakes were placed along each transect at 20 m intervals. All horizontal measurements are based on the ocean shoreline, at the time of survey, at the zero point. A mention of "250 m" refers to a point 250 m west of the ocean shoreline. Horizontal distances are measured in meters and vertical distances in feet.

Standard surveyor's instruments (a telescopic level and graduated rod) and methods were used to determine the relative elevation of various points along each of the four transects. On irregular terrain, elevations were determined at intervals of 5 m or less along each transect. On flat or uniformly sloping terrain, elevations were measured at intervals of 10 or 20 m. Computations for determining elevation above mean sea level were based on United States Coast and Geodetic Survey bench markers of known elevation.

Using a horizontal scale of $1/5'' = 1$ m and a vertical scale of $1/5'' = 1$ ft, the topographic profile of each transect was then plotted on quadrille paper. The same paper was then used as a score sheet for recording ocular estimates of cover for each species present in a series of meter-square quadrats arranged contiguously along each transect. A 20 m tape was stretched between successive stakes and 2 m long rods, marked in decimeters, were laid at right angles to the tape to provide a convenient grid reference for estimating percentages of cover.

Each species was rated individually and scored without separation into strata. Consequently, some quadrats scored more than 100% cover. Overlap was not measured directly, but it is implied by any rating in excess of 100%. Conversely, a rating of less than 100% implies space from the ground upward through all the strata present.

Boundaries and transitions (or ecotones) between plant communities were marked on the score sheets as they were encountered in the field. The frequency of occurrence in quadrats and the average cover per quadrat for each species in each plant community traversed were computed from these data. Average frequency and cover data derived from these computations have already been used in describing the various classes of mapping units (page 4).

RESULTS

The topographic profiles and plant communities traversed are indicated for all four transects in Fig. 17. Data derived from quadrat analyses are tabulated separately for each transect in Tables 7 through 10. Future references are made only to transect number and imply that both Fig. 17 and the appropriate table or tables should be consulted for verification. Cover values for each species in each community traversed have been rounded to the nearest whole number except in the totals column. Total percent cover and percent frequency on each transect were computed from the total number of quadrats sampled on each transect.

These data provide a measure of each community's floristic composition. They also indicate the distribution of each species population in relation to topographic profiles and in relation to the various vegetation mapping units. Several significant relationships between vegetation patterns and topographic patterns are illustrated by these data.

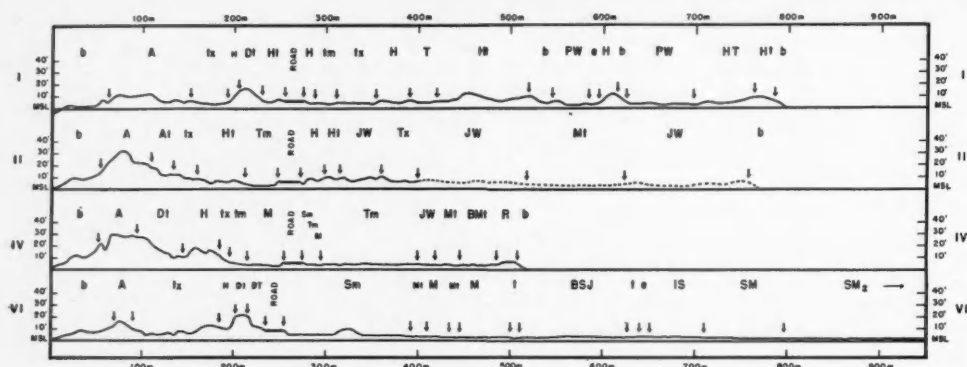(a) Topographic and vegetational patterns are

FIG. 17. The distribution of individual plant communities (mapping units) along 4 contrasting topographic profiles. The letter symbols refer to the mapping unit classes listed in Table 4 except b = bare sand, and e = ecotone. See Fig. 2 for the location of the transects. The vertical scale is approximately three times the horizontal scale. The dotted line indicates estimated elevation. MSL = Mean sea level.

TABLE 7. Percentage of cover contributed by the species present in the mapping units traversed by Transect I (Fig. 17). Species are listed in the order they were encountered from east to west. Symbols refer to the vegetation mapping units traversed. %C, percent cover; %F, percent frequency; t, trace.

TRANSECT I:	A	tx	H	Dt	Ht	H	tm	tx	H	T	Ht	PW	e	H	PW	HT	Ht	b	%C	%F
Ammophila breviligulata	2	4	1	1	4													t	0.71	14.8
Euphorbia polygonifolia	t			1															0.04	3.5
Cakile edentula	t																	t	0.20	1.3
Solidago sempervirens	1				t													t	0.20	4.5
Lathyrus japonicus		t	1																t	0.6
Lechea maritima		t											t						t	0.6
Cyperus grayii		t	2	1				t			1			t					0.20	5.4
Rhus radicans		23		16	11		1	t		t	t					t	t	t	2.43	12.6
Myrica pensylvanica		14		12			3	9	3	t	t				t	t	12	t	2.83	10.5
Smilax rotundifolia		6		7			9	27	7	7	1			t	1	3	t		3.91	23.8
Prunus serotina		3															t		0.20	0.6
Vaccinium corymbosum		7					65	13		14		38			40				9.51	18.4
Rosa virginiana		t					t												0.02	0.7
Prunus maritima		5		27	4	11	2									20		5	2.25	6.6
Parthenocissus quinquefolia		t		2	2											t			0.16	2.2
Hudsonia tomentosa			19		6	61	1	18			11			t	24	5	4		4.95	28.9
Andropogon scoparius			7	1	5	2	t	2			1								0.72	6.3
Opuntia humifusa				1				t	t										0.06	1.0
Cladonia spp.					t			t	t				14	1		t			0.22	9.3
Rumex acetosella				t			t												t	1.2
Kalmia angustifolia							13	2				31	t		26	4			5.94	15.8
Rhus copallina							2	5											0.38	2.1
Amelanchier canadensis							2		1										0.13	0.6
Osmunda regalis							5												0.19	0.9
Juniperus virginiana							t			24	1				10				2.09	3.7
Quercus ilicifolia								8	1		4	t	26	2	2	35			4.93	9.4
Pinus rigida								5	1		4	48	3	1?	45				9.45	12.1
Panicum amarum								t						t	t				0.02	1.9
Ilex opaca										32	2					9			2.59	3.9
Quercus marilandica										1				3	1				0.04	1.0
Sassafras albidum										1	7								1.07	1.6
Chamaecyparis thyoides												22			17				3.37	7.5
Gaylussacia frondosa													1		2				0.28	0.7
Ilex glabra													t		t				t	0.4
Quercus phellos																8			0.67	0.7
Totals	4	64	30	69	33	74	100	73	29	81	32	143	43	41	135	74	37	6	59.94	....

(+Spartina patens & Salsola kali)

similar but not identical. Both topographic and vegetational zones are recognizable and sometimes coextensive, but these zones do not always have sharp boundaries. Certain zones may be absent, or narrow, or poorly developed in one place and exceptionally conspicuous, broad, or well developed in another place. The interzonal and intrazonal diversity in the distribution of topographic facets (the basic area units

TABLE 8. Percentage of cover contributed by the species present in the mapping units traversed by Transect II (Fig. 17). Species are listed in the order they were encountered from east to west. Symbols refer to the vegetation mapping units traversed. %C, percent cover; %F, percent frequency; t, trace.

											TOTALS	
TRANSECT II:	A	At	tx	Ht	Tm	e	H	Ht	JW	Tx	%C	%F
Cakile edentula	t										0.03	2.0
Ammophila breviligulata	8	3		t				t			1.68	26.6
Solidago sempervirens	1	4	1	1							0.59	13.8
Euphorbia polygonifolia	t										0.02	2.1
Rhus radicans		20	70	3	3	41	1	2	10	11	10.68	40.7
Parthenocissus quinquefolia		t	12						t	1	1.11	7.2
Rosa virginiana			2		15	t			t		0.31	5.9
Myrica pensylvanica			7		6	t		4	4	31	6.49	23.4
Smilax rotundifolia			1			t		9	10	3	2.85	27.2
Hudsonia tomentosa				19			12	1		1	4.09	26.6
Cyperus grayii				t			t	t			0.02	1.8
Juniperus virginiana				1	1			2	90	19	14.80	16.8
Ilex opaca				5	3			16	26	7	6.03	10.5
Cladonia spp.				3			2	1			0.75	7.2
Panicum amarum				t			t				0.03	1.8
Vaccinium corymbosum					75	5					7.99	10.0
Amelanchier canadensis					9				3	10	2.58	5.0
Osmunda regalis					1						0.09	2.4
Osmunda cinnamomea					t						0.01	0.6
Acer rubrum					6						0.61	0.9
Kalmia angustifolia					5						0.52	1.5
Rubus flagellaris								4			0.16	1.5
Opuntia humifusa								2	1		0.41	2.1
Vaccinium vacillans								t	4		0.57	2.7
Prunus serotina								2	20	12	4.10	7.2
Prunus maritima										20	2.28	4.5
Smilax glauca										2	0.25	2.4
Populus gileadensis										3	0.30	0.9
Totals:	9	27	92	32	124	46	15	43	170	120	69.35	....

of topography) and plant communities (the basic area units of vegetation) is such that both occur in patterns aptly described as zoned mosaics.

On transect I, the shore zone (0-60m) has a characteristic configuration but relatively low elevation. The primary dune zone (60-192m) is divisible into a broad foredune ridge (60-125m) and a shallow backdune swale (125-192m). The Dunegrass or herbaceous vegetation zone exhibits effusion, but only the easternmost part (60-100m) is vigorous. The remainder (page 23) is degenerate. The secondary dune zone (192-780m) begins with a more or less typical secondary foredune and extends to the edge of a narrow bayshore zone (780-785m) represented only by a sandy beach. The secondary backdune zone is exceptionally broad and has a much higher than average elevation. The shrubby vegetation zone (approx. 153-500m) and the arborescent vegetation zone (approx. 500-780m) are unconsolidated and frequently interrupted by Beach Heather communities and Beach Heather-Thicket Mixtures. The shape of the westernmost dune (725-780m) suggests a moderate amount of dune-building made possible by the narrow sandy bayshore zone which is exposed to the prevailing westerly winds.

The distribution of plant communities and topographic facets on the other three transects is similarly diversified, and the boundaries between topographic and vegetational zones are equally broad and indistinct. One exception is the shore zone. It varies somewhat in configuration and especially in elevation; but, on all four transects, it has sharp eastern and western boundaries.

The primary dune zone of transect I is similar, in most respects, to that of transect VI. Both end at the base of a secondary foredune, and both have relatively low foredunes and swalelike primary backdune areas. Like similarities are noted in comparing transects II and IV both of which have high primary foredunes whose backslopes terminate at the edges of depressions. The notch in the primary foredune of transect IV is a blowout channel. The relatively high dune which interrupts its backslope lies at the end of another blowout channel which breeches the primary foredune ridge about 50 m north of the transect.

In comparing secondary dune zones, transects I and VI have similar secondary foredunes while secondary foredunes are absent from transects II and IV. The secondary backdune area of transect I is similar to that of transect II except that a slightly higher elevation is indicated for the latter. The secondary backdune area of transect IV is relatively low and terminates (arbitrarily) at the edge of a moderately wide (416-610m) bayshore zone which is more or less typical for this part of the bar. That of transect VI, on the other hand, is interrupted by a sandy ridge which may represent a former shoreline. The bayshore zone on this transect (VI) is exceptionally broad, but it is difficult to locate the boundary between this zone and the secondary backdune zone. The boundary between peaty and sandy substrata is at 650m, but the area between 310 and 650m is underlain by deposits of peat, and the vegetation zones commonly associated with Salt Marsh succession all lie west of 510m.

These comparisons give some indication of the range of topographic diversity and the ways in which topographic and vegetational patterns are associated. Proceeding from east to west, this association generally becomes less distinct, and it becomes more difficult, in most cases, to locate vegetational boundaries along obvious topographic lines.

(b) Similar plant communities (indicated by their relegation to the same mapping unit class) tend to occupy similar topographic facets. Dunegrass communities, for example, occupy the primary foredunes of all four transects. The several facets of the secondary foredunes encountered on transects I and VI are occupied by similar communities: Beach Heather on the foreslopes, Low Dune Thickets on the tops, and Low or High Dune Thickets on the backslopes. Beach Heather communities may occur in either the primary or the secondary backdune areas, but they are restricted to protected dunes above 5 ft elevation. Fresh Marsh communities and various kinds of Marsh-Thicket Mixtures are encountered only on flats or in

TABLE 9. Percentage of cover contributed by the species present in the mapping units traversed by Transect IV (Fig. 17). Species are listed in the order they were encountered from east to west. Symbols refer to the vegetation mapping units traversed. %C, percent cover; %F, percent frequency; t, trace.

TRANSECT IV:	A	Dt	H	Dt	H	tx	tm	M	Mt	Sm	Tm	M	Tm	JW	Mt	BMt	R	TOTAL %C	%F
Ammophila breviligulata	9	1	1															0.91	8.3
Cakile edentula	t	1																0.04	2.3
Solidago sempervirens	t	1	6															0.14	2.9
Parthenocissus quinquefolia		21		15		11	1											2.03	8.9
Prunus serotina		18	1	36		32	2											2.93	6.9
Rhus radicans				2		2	36	7	14	9		2	7	15	28	41	30	12.03	59.0
Myrica pensylvanica		3	t			3	t						5	10	8	3		2.56	14.2
Juniperus virginiana		t											9	47	8	5		2.13	10.6
Hudsonia tomentosa			43		46													4.39	8.7
Amelanchier canadensis						3												0.23	0.9
Smilax rotundifolia							15		2	99	52	1	31	2	t			11.26	34.5
Vaccinium corymbosum							39				42		26					1.75	3.4
Osmunda cinnamomea							6				20	50						1.45	1.8
Dryopteris thelypteris							4					50	3	2	51	3		5.43	21.4
Sphagnum spp.							13	43				t	t					4.54	10.3
Rosa rugosa							3	10	71				3	48	20	2	3	5.74	21.8
Osmunda regalis							t						t					0.03	0.6
Hibiscus palustris							t	20				t			2	t		0.68	6.9
Hypericum virginicum								40										0.66	6.4
Juncus canadensis								3								27		2.64	12.2
Scirpus americanus								2										1.28	7.8
Vaccinium macrocarpon								t										0.17	1.4
Acer rubrum								8			20		1					1.37	5.0
Ilex opaca													13					3.24	5.0
Clethra alnifolia												1	1					0.30	2.0
Baccharis halimifolia																41	6	3.62	9.2
Typha latifolia																1		0.09	5.3
Phragmites communis																t	67	3.28	6.4
Polygonum pensylvanicum																1		0.07	0.4
Zostera marina																	t	.....	....
Totals:	10	45	44	58	46	51	112	133	87	108	134	105	99	126	119	124	106	75.74	....

depressions below 4 ft elevation. Salt Marsh communities, represented only on transect VI, occupy a peaty flat which is nowhere more than 2 ft above mean sea level. Pine Woodland occurs twice on transect I—both times in depressions at or below 3 ft elevation. Red Cedar Woodland, on the other hand, occurs on dunes or on flats at or above 5 ft elevation. Both woodland types are confined to secondary backdunes.

(c) Similar topographic facets on different transects, may be occupied by different kinds or combinations of plant communities. The primary backdune zones of transects I and VI, for example, are somewhat similar in contour. The swalelike portions of both are occupied by Low Xeric Thicket. The long backslopes of high primary foredunes on transect II and IV are both occupied by a complex Dunegrass-Beach Heather-Low Thicket Mixture. The components of this mixture conform more or less with contrasting topographic facets on the two transects. Both backslopes terminate in depressions which are approximately 40 m wide and 3.5 ft above mean sea level. The depression on transect II is occupied by a dense High Mesic Thicket community dominated by *Vaccinium corymbosum* while that of transect IV is occupied by a Fresh Marsh community dominated by *Hypericum virginicum* and *Hibiscus palustris*. The boundaries of both communities correspond closely to a contour line (determined by level and rod) between 3 and 4 ft elevation. The secondary backdune zones of transects I and II are topographically similar but vegetationally dissimilar. On transect I, nearly all the areas above 5 ft elevation are occupied by Beach Heather, and the areas below 5 ft are occupied by woody vegetation. On transect II, the areas above 5 ft are occupied either by Beach Heather or Red Cedar Woodland, and the areas occupied by Marsh Thicket appear to be below 5 ft elevation. The secondary backdune zones of transects IV and VI are also similar. Both are sandy flats interrupted in places by depressions. The depressions on both transects are occupied by Fresh or Brackish Marsh, but the higher ground on Transect IV is occupied by High Mesic Thicket and Red Cedar Woodland while that on transect VI is occupied primarily by Greenbrier Thicket.

(d) Some plant species appear to be restricted to a particular kind of plant community which, in its turn, is apparently restricted to a particular kind of topographic facet. Others are virtually ubiquitous and occur abundantly in many kinds of plant communities on a variety of topographic facets. The relative cover contributed by the plant species encountered in the various communities traversed by these four transects is shown in Tables 7 through 10.

TABLE 10. Percentage of cover contributed by the species present in the mapping units traversed by Transect VI (Fig. 17). Species are listed in the order they were encountered from east to west. Symbols refer to the vegetation mapping units traversed. %C, percent cover; %F, percent frequency; t, trace.

TRANSECT VI:	A	tx	H	Dt	DT	Sm	Mt	M	Mt	M	t	BSJ	t	e	IS	SM	SM$_2$	TOTALS %C	TOTALS %F
Cakile edentula	1																	0.02	1.2
Rhus radicans	t	34		2	8	t	28	24	26	11	89	36	83					12.53	35.6
Parthenocissus quinquefolia	1	12		38	6	2	3											2.12	16.5
Ammophila breviligulata	17	t																0.45	2.8
Solidago sempervirens	2	1												6				0.19	2.6
Myrica pensylvanica		28		6	3			1	21		13	6	6					4.28	12.8
Smilacina stellata		8		4	t													0.85	1.8
Prunus serotina		17		24	83													4.29	7.9
Smilax rotundifolia		2	t	t	1	93	48											15.29	20.6
Amelanchier canadensis		1				1				1	1							0.32	1.7
Panicum virgatum		1	2	1	3	t						t						0.30	3.4
Hudsonia tomentosa		t	33															0.60	1.7
Ilex opaca		2			6	t												0.49	1.5
Juniperus virginiana		t			1	1						5	t					0.83	1.4
Opuntia humifusa				1														t	0.2
Rhus copallina						1	4					t						0.32	2.3
Vaccinium corymbosum						6												0.99	1.9
Acer rubrum						t	12	14	25	t								0.89	4.2
Dryopteris thelypteris							25	51	4	t			1					1.82	4.6
Scirpus americanus								5	1				t					0.14	3.0
Hypericum virginicum								1	t									0.03	1.6
Spartina patens									52	98	12	69		95	96	80	5	30.34	50.5
Sphagnum spp.										5								0.29	3.7
Baccharis halimifolia											3	31		29				4.15	7.6
Eupatorium spp.												1	11					0.25	6.0
Andropogon scoparius var. abbreviatus												t						t	0.4
Iva frutescens														43	24	t		1.95	5.8
Spartina alterniflora																12	20	5.98	25.0
Salicornia europaea																t	t	t	0.7
Salicornia virginica																t	75	18.47	25.0
Totals:	21	97	35	76	111	109	120	96	129	115	118	148	101	173	120	92	100	107.99	....

These data give some idea of species' population patterns in relation to topography and plant communities.

In spite of appearances to the contrary, very few species are totally restricted to a single kind of topographic facet. *Ammophila breviligulata,* for example, is almost always present and usually the dominant species on the tops of primary foredunes, but it also occurs in more mesic primary backdune swales (Fig. 10). *Spartina patens* is almost always present and commonly the dominant species in Salt Marsh communities which are restricted to intertidal peat flats. It is also the dominant species in at least one Fresh Marsh community (transect VI:445-500m) and in most Brackish Marsh communities (page 10). It has been found, however, in association with *Hudsonia tomentosa* on xeric dunes; and in one quadrat (transect I:781m), healthy plants of *Spartina patens* and *Ammophila breviligulata* were found side by side.

Dryopteris thelypteris, Hibiscus palustris, Hypericum virginicum, Rosa rugosa, Baccharis halimifolia, Acer rubrum, and many other herbaceous and woody species are apparently restricted to hydric sites near the water table and thus to Fresh Marsh, Brackish Marsh, or Marsh Thicket communities. *Cakile edentula, Euphorbia polygonifolia, Hudsonia tomentosa, Artemisia stelleriana, Prunus maritima, Quercus ilici-folia, et al.* exhibit similar apparent restriction to xeric sites. Still other species, e.g., *Juniperus virginiana, Ilex opaca, Prunus serotina,* and *Amelanchier canadensis,* are found commonly and abundantly on both mesic and xeric sites provided by a variety of topographic facets occupied by a variety of community types.

Three shrub species—*Rhus radicans, Myrica pensylvanica,* and *Smilax rotundifolia*—are especially abundant and widespread in relation to plant communities and topographic facets. The first two show signs of a bimodal distribution by reaching peaks of importance (as shown by relative cover) first in open communities occupying xeric habitats and again in open communities occupying mesic or hydric habitats. *Smilax* is quite widespread and can be found in most kinds of plant communities, but it reaches a pronounced peak of importance only in a few mesic habitats.

Different species' population patterns show varying degrees of association with topographic and vegetational patterns. Some groups of species have similar population patterns, but no two are exactly alike.

DISCUSSION

The zoned mosaic patterns of vegetation and topography, which were described in the earlier parts

of this report, have been illustrated in this study by showing some of the minute details of topographic profile and vegetational distribution along four contrasting transects. The working hypothesis (page 21) that the complex vegetation patterns of Island Beach conform closely to topographic conditions has been largely confirmed and elucidated.

The recurrence of similar or virtually identical plant communities on similar or virtually identical topographic facets has been demonstrated in this study, and it clearly indicates an intimate relationship between vegetation and topography. Community-facet relationships are especially constant in the case of strictly herbaceous communities which occupy facets characterized by severely limiting enironvmental conditions. Virtually all primary foredunes, for example, are occupied by Dunegrass communities; true Salt Marsh communities occur only on intertidal peat flats; and nearly all the Reedgrass communities of any importance occur on low, sandy ridges, parallel to the bay shoreline.

The constancy of these three reciprocal community-facet correlations is hardly surprising. It has already been shown that the facets in question—primary foredunes, intertidal peat flats, and bayshore sand ridges—are all formed by physiographic processes which require the participation of both physical and biotic forces. The very existence of these vegetation-environment units is dependent on the maintenance of a dynamic state of vegetational and environmental equilibrium.

Other community-facet correlations are just as striking as regards the coincidence of topographic and vegetational boundaries, but the vegetation is not always the same kind. Fresh Marsh communities, for example, always occur in depressions or on flats below 4 feet elevation, but other facets of the same kind may be occupied by Low Marsh Thicket, Low or High Mesic Thicket, or even Pine Woodland. Beach Heather communities are found only on protected dunes above 5 ft elevation. Similar facets, however, are occupied by a variety of different Beach Heather-Thicket Mixtures, and in some areas by Red Cedar Woodland. Community-facet relations of this nonreciprocal kind are strongly suggestive of successional change, and they may be of some use in tracing successional trends and relationships among communities occurring on the same kinds of facets.

In addition to these two varieties of community-facet correlations, termed reciprocal and nonreciprocal, it has been demonstrated that each vegetationally important species' population is distributed differently in the spectrum of plant communities and topographic facets. If each population pattern is interpreted as a reflection of that population's ecological amplitude in respect to total environment, the vegetation pattern is seen to represent the summation of all plant responses to total environment. If this is true, the vegetational pattern is a true reflection of the environmental pattern. The fact that the vegetational pattern is closely correlated with topography clearly

emphasizes the value of topography, in this area at least, as an index to total environment.

The next logical step in testing the hypotheses and tentative conclusions thus far proposed is to examine the relationship between topography and limiting factors. An analysis of these relations should prove to be useful in the characterization of the environmental pattern to which plants respond. This, in turn, should bring us closer to an expression of the essential character of the vegetation-environment system.

TOPOGRAPHY AND LIMITING FACTORS

While topography is a controlling factor and therefore considered to be a good index to total environment, it does not enter directly into plant-environment reactions. In order to clarify the nature of community-facet relationships, the relationships between topography and environmental factors were examined. The principal environmental factors (or groups of factors) which are apparently controlled by topography and capable of limiting the distribution of plants on Island Beach are those concerned with the amount or intensity of sand movement, available soil moisture, ground water salinity, and windborne salt spray. Sand movement has already been considered as part of a physiographic process operating chiefly in the zone of primary dunes. The purpose of the study described in the following pages was to measure or obtain an index to the amount or intensity of available soil moisture, ground water salinity, and windborne salt spray under different topographic conditions. Some of the results of this study have already been cited.

METHODS

(a) Soil Conditions—Test borings 5 ft deep and 3 in. in diameter were made with a bucket-type soil auger at points along transects I, II, IV, and VI and in a variety of habitats not traversed by these transects. The distance of each point from the shoreline, its elevation above mean sea level, and the kind of vegetation surrounding it were noted. The depth and appearance of various layers (not true soil horizons) pierced by each boring were described in the field. At points where the water table was encountered, ground water was allowed to collect in the holes. The distance from the surface of the ground was measured and recorded as the depth of the water table. Samples of ground water were collected for salinity determinations which were made by the Knudsen method (Woods Hole Oceanographic Institution 1946). Water samples were also collected for this purpose from the ocean, the bay, and from borings made in a variety of habitats in different parts of the study area.

(b) Salt Spray Distribution—The distribution of salt spray in relation to topography was measured by exposing cheesecloth salt traps to various weather conditions at stations along several transects. Similar studies have been made previously by Oosting

and Billings (1942) and by Boyce (1954). The salt traps used in this study were made by sewing a good grade of cheesecloth to wire frames made by stretching coat-hangers into squares. A target area of one square decimeter was marked with indelible ink in the center of each salt trap.

To avoid contamination before exposure, the salt traps were stored in sealed plastic or paper bags. During exposure they were attached to wooden stakes by means of two fencing staples. After exposure, only the target areas were collected, and each one was placed in a separate, waxed-paper sandwich bag which was labeled for proper identification.

In the laboratory, each target area was placed in a beaker containing 50 ml of distilled water and 0.5 ml of 16% potassium chromate solution and allowed to soak for 10 minutes or more. The resulting solution was titrated to a pale red end-point with a solution of 0.02 normal silver nitrate. The chloride content of test samples can be computed from atomic weights; but, in this case, it was more practical to use a correction factor ($F = 1.2762$), based on the Knudsen method cited above, to obtain total salinity. Thus, milliliters of silver nitrate times 1.2762 is equal to milligrams of salt per square decimeter of cheesecloth. The same figures can then be interpreted as kilograms per hectare, and grams per square meter can be determined by moving the decimal point one place to the left.

Transects III and V were established in June, 1956, for the express purpose of measuring the distribution of salt spray in relation to topography. Stations were located at 9 points along each transect —one each on the ocean shore and the bay shore and then at alternately high and low points in between. Two traps were exposed at each station—one at 1 ft above the surface and the other at 3 ft above the surface.

Early results suggested that the measurement of salt spray intensity at canopy height might be desirable. Stations of the proper kind could not be established, however, until the vegetation transects were laid out in July, 1957. Salt traps were then exposed 1 ft above canopy height at various stations on transects I, II, IV, and VI during several northeasterly storms. Many of the traps placed in trees or attached to shrubs were blown down by strong winds. On other occasions, the traps were washed free of salt by heavy rains. Only one run was successfully completed during which salt traps were exposed simultaneously at the canopy height stations on all 4 transects.

RESULTS

(a) Soil Conditions—The depth of the water table below the surface was found to vary directly with surface elevation. The elevation of the water table (surface elevation minus depth to water table) above mean sea level is therefore relatively constant. The mean water table elevation, computed from measurements made at 85 stations in a variety of habitats,

was 2.2 ± 0.5 ft above mean sea level in August, 1957, following 7 weeks of drought. Observations and measurements in March and April, 1958, indicate that the water table elevation in early spring is at least 1 ft higher than in late summer.

At the time of survey, moist sand was invariably encountered a few inches below the surface. This was true even on high, exposed dunes. At lower elevations, especially at stations where the water table was encountered within 5 ft of the surface, there was a marked and visible increase in the moisture content of sand with increasing depth. At higher elevations, the moisture content of subsurface sand was very low, just enough to impart a slightly darker color and a slightly more cohesive consistency than dry sand, and there was no apparent increase in moisture content with increasing depth. Slight color changes, from white to gray to tan, with increasing depth were noted at most stations of intermediate elevation but not on high dunes or in low depressions.

Surface layers of peat, having an average depth of 25 in. were found in association with tidal-marsh communities (transect VI:690-950m); and buried layers of peat, varying in thickness from 4 to 28 in., were found under other communities (transect VI: 310-690m). Most Fresh Marsh and Brackish Marsh communities are underlain by shallow (2-10 in. layers of peat. One buried layer of peat (transect I:240m) was found unexpectedly under a Beach Heather-Low Thicket community and another (page 11) under a Cranberry Bog community.

Dense root mats were found on all 4 transects, and elsewhere too, in association with shrubs and trees whose roots develop abundantly in the upper few inches of the mineral soil. Buried root mats also were encountered in a few places on transects II and IV. The mor type of litter is rather sparse, and for the most part, it is limited to dense thicket or woodland vegetation.

Salinity determinations indicate no more than a negligible amount of salt in the ground water under most habitats. Ground water samples collected from mesic sites occupied by Fresh Marsh, Low Marsh Thicket, Low and High Mesic Thicket, Red Cedar Woodland, and Pine Woodland showed no reaction when tested for chloride or indicated a total salinity of less than 2 parts per thousand. The salinity of ground water collected from areas mapped as Brackish Marsh (and related thicket types) ranged from 3 to 20 parts per thousand (page 10), but the modal range is about 6 to 12 parts per thousand. In contrast to the salinity of bay water (26.6) and the salinity of ocean water collected from the surf (31.5 parts per thousand), these figures do not indicate an appreciable amount of salt. In contrast to the variability of ground water salinity in most areas, there was a conspicuous salinity gradient on transect VI (see Fig. 17) which can be summarized as follows: 450m—3.0 parts per thousand, 510m—5.2, 550m—7.0, 590m—8.6, 650m—18.3, 730m—26.7, 850m—32.0, and 950m 35.8.

TABLE 11. Milligrams of salt per square decimeter recovered from cheesecloth salt traps exposed at stations on Transects III and V to the weather conditions indicated below.

TRANSECT III:

Station*			Run 1		Run 2		Run 3		Run 4		Run 5		Run 6		Totals		Per Cent	
#	D	E	1'	3'	1'	3'	1'	3'	1'	3'	1'	3'	1'	3'	1'	3'	1'	3'
1	50	12	1	2	39	68	64	76	56	94	119	134	415	585	695	960	72	100
2	80	23	1	1	34	42	42	54	60	71	82	122	363	386	582	675	61	70
3	90	34	1	1	12	24	8	46	41	81	74	113	20	183	156	447	16	47
4	120	14	1	1	10	14	6	27	28	55	31	53	53	75	128	225	13	23
5	165	20	1	1	25	32	31	39	59	72	86	79	112	142	313	365	33	38
6	215	7	1	1	5	8	9	24	19	36	25	45	26	37	84	151	9	16
7	285	13	1	1	5	5	7	31	38	47	44	57	38	59	132	200	14	21
8	325	6	0	1	1	4	7	15	9	20	10	22	22	42	49	103	5	11
9	385	4	1	1	1	1	1	3	1	2	1	1	2	7	5	14	1	1
Totals:			5	9	131	197	175	315	311	477	471	626	1051	1516	2144	3140	—	—

TRANSECT V:

#	D	E	1'	3'	1'	3'	1'	3'	1'	3'	1'	3'	1'	3'	1'	3'	1'	3'
1	30	12	2	4	37	60	30	57	62	100	120	130	396	553	647	904	72	100
2	60	23	1	1	41	65	38	55	45	87	97	109	135	155	357	472	39	52
3	110	36	1	1	1	1	3	11	19	59	59	66	104	106	187	244	21	27
4	170	12	1	1	1	15	2	20	3	24	5	24	38	48	49	132	5	15
5	250	23	1	1	16	34	21	32	27	40	35	41	99	19	108	167	12	18
6	270	16	1	1	1	1	2	2	16	19	6	9	14	20	38	52	4	6
7	435	20	1	1	1	7	1	11	7	15	6	14	3	1	17	48	2	5
8	485	12	1	1	1	0	1	1	1	1	2	1	4	8	7	10	1	1
9	735	6	1	1	1	3	2	7	1	1	2	2	1	1	7	13	1	2
Totals:			7	11	98	186	99	195	180	346	332	395	703	911	1517	2044	—	—

			Run 1		Run 2		Run 3		Run 4		Run 5		Run 6	
Hours exposed			48		24		48		48		24		168	
Wind			W-SW Light		E-NE Strong		E-NE Moderate		NE Moderate		NE Moderate		Variable Variable	
Precipitation			Some Fog		None		Some Fog		None		Constant Fog		Light Rains	

*   #—Number of salt trap station (See Fig. 18).
D—Distance in meters west of the ocean shoreline.
E—Elevation in feet above mean sea level.

(b) Salt Spray Distribution—The results of 6 periods of salt trap exposure on transects III and V are summarized in Table 11 and Fig. 18. Each period of exposure is referred to as a "run." Each run represents the simultaneous exposure of all the salt traps on both transects to the same weather conditions. Salt spray is not carried far by thermal sea breezes (Boyce 1954), so most of the runs were made during periods of northeasterly winds in excess of 10 mi. per hr. The 6 runs are arranged in increasing order of total salt recovery, and all data are expressed as milligrams of salt recovered per square decimeter of cheesecloth.

These data show a marked lack of constancy as regards the total amount of salt recovered from salt traps at particular stations and the kind of weather to which they were exposed. The relative amounts of salt deposited on traps at different stations on the same transect, however, are constant to a marked degree. Traps exposed 1 ft above the surface, for example, almost always receive less salt spray (32% less on the average) than traps exposed 3 ft above the surface. Decreasing amounts of salt were recovered after most runs from stations at increas-
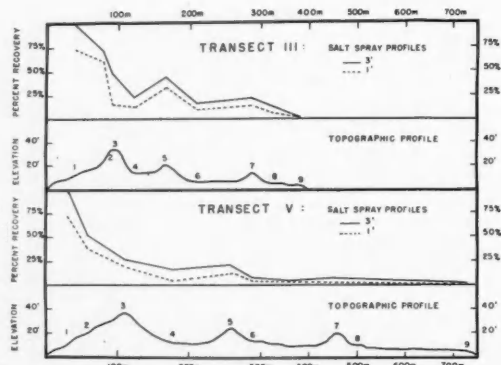

FIG. 18. Topographic profiles and relative intensity of salt spray deposition at stations indicated on transects III and V. For the location of these transects, see Fig. 2. Percentages of salt spray recovery are based on data given in Table 11.

ing distances from the shoreline. The difference is considerably greater for stations at low elevations than for stations at higher elevations above

mean sea level, and it is more noticeable on transect V which is longer than transect III. Each transect has 3 pairs of stations placed with one member of the pair on a dune crest and the other member in a protected swale immediately to the west. By comparing stations 3 and 4, 5 and 6, and 7 and 8 on each transect, it can be seen that protected stations at lower elevations always receive less salt spray (50% less on the average) than stations immediately to the east and at higher elevations above mean sea level, and this relationship holds true for both the 1 ft and the 3 ft level.

Table 12 shows the results of a single run during which salt traps were exposed simultaneously at all the canopy height stations on transects I, II, IV, and VI. All these stations were located at least 1 ft higher than the canopy of the surrounding vegetation and, therefore, generally at increasingly higher elevations from east to west. These data indicate a more gradual decrease in salt spray intensity with increasing distance from the ocean shoreline than is indicated by data obtained from stations near the ground on transects III and V. The apparent rate of decrease at canopy height is relatively slow from the shore to about 350m and relatively fast from 350m to points farther west.

Table 12. Milligrams of salt per square decimeter recovered from cheesecloth salt traps exposed for a 24-hr period of light to moderate northeasterly winds at the canopy height salt trap stations indicated. #—Number of salt trap station, D—Distance in meters west of the ocean shoreline, E—Elevation in feet above mean sea level, S—Milligrams of salt per square decimeter of cheesecloth, %—Percent of salt recovered from the station nearest the ocean shoreline.

#	Transect I				#	Transect IV			
---	D	E	S	%	---	D	E	S	%
1	40	6	48	100	1	50	18	50	100
2	70	15	45	94	2	65	32	47	84
3	100	15	33	69	3	95	22	23	46
4	135	15	29	60	4	160	18	19	30
5	180	10	28	58	5	210	12	13	26
6	205	19	26	54	6	260	12	15	30
7	240	9	14	29	7	370	20	12	24
8	290	12	16	33	8	470	12	6	12
9	275	16	15	31	9	510	5	3	6
10	390	22	20	42					
11	450	15	11	23		Transect VI			
12	520	24	9	19	#	D	E	S	%
13	610	24	9	19					
14	710	22	7	15	1	60	12	51	100
15	780	11	1	2	2	80	16	30	59
					3	130	12	22	59
	Transect II				4	180	19	24	47
#	D	E	S	%	5	210	25	22	43
					6	330	13	4	8
1	35	12	47	100	7	330	26	22	43
2	75	35	31	66	8	450	13	9	18
3	140	12	23	49	9	550	13	8	16
4	200	12	24	51	10	630	10	5	10
5	300	14	20	43	11	730	6	6	12
6	350	28	11	23	12	830	6	7	14
7	450	31	7	15	13	930	6	5	10
8	600	31	7	15	14	1030	6	5	10
9	600	5	1	1	15	1030	10	6	12

DISCUSSION

(a) Soil Conditions—Except for marshy areas, the substratum of Island Beach is siliceous sand of high porosity and excessive drainage. Although not measured directly, the amount of moisture retained by sand lying well above the water table is probably not adequate to sustain the growth of shallow-rooted mesophytes. The water table appears to be lowest (2.2 ft above mean sea level) in late summer and highest (about 3.5 ft above mean sea level) in early spring. Because the water table is relatively level, it is possible to estimate its depth below any surface of known elevation. Most hydrophytes, e.g. *Vaccinium corymbosum, Dryopteris thelypteris*, etc., are restricted to sites below 5 ft elevation which are about 1.5 to 3.0 ft above the water table. Many xerophytes, e.g., *Hudsonia tomentosa, Prunus maritima*, etc., on the other hand, are restricted to sites above 5 ft elevation. These and similar considerations provide a strong case for the conclusion that the availability of moisture is closely associated with elevation. Thus, the soil moisture gradient varies inversely with the topographic profile.

Substratum layers formed by vegetation, e.g., peat deposits and root mats, found under layers of sand may provide evidence useful in a more refined reconstruction of the physiographic and successional history of certain parts of the study area. Thickets, for example, which form root mats at the soil surface, may be partly covered by windblown sand. In a similar manner, the peat formed by Salt Marshes may be covered by sand deposited during storms by high winds and tidal waves. Thickets may survive some burial by sand, but the same amount of deposited sand can produce radical changes in the Salt Marsh (page 10) environment.

The few measurements of ground water salinity made to date are sufficient to suggest that soil salinity is important as a limiting factor only in habitats which are exposed to tidal flooding. Changes in soil salinity may control the rate and course of some of the successional changes experienced in habitats (page 10) which by one means or another are removed from the influence of tidal flooding.

(b) Salt Spray Distribution—As indicated by the data presented above (Tables 11 & 12), the distribution of salt spray is also under the controlling influence of topography. The amount of salt spray deposited on plants probably depends on the interaction of a great many environmental factors not taken into account in this study, but the parallel between topographic profiles and the relative distribution of salt spray (Fig. 18) is quite striking. The intensity of salt spray deposition decreases with increasing distance from the ocean shoreline. It tends to increase, however, with increasing elevation and increasing height above the ground. Since the height of vegetation tends to increase from east to west, the decreasing intensity of salt spray deposition with increasing distance from the shoreline is much less pronounced at the top of the vegetation canopy than it

is near the surface of the ground. The rapid decrease in salt spray intensity near the ground suggests that low growth-forms are adapted to escaping high salt spray intensity. The influence of topography on soil moisture and on salt spray distribution is such that moisture increases and salt spray intensity decreases with increasing distance from the ocean shoreline and decreasing elevation above mean sea level.

In general, it may be concluded that the influence of topography on the principal limiting factor gradients is such that each topographic facet is characterized by a different combination of environmental conditions. Many combinations are possible, but the number of significantly different combinations is definitely limited by the relative degree of topographic diversity. In this environment, at least, topography serves admirably as an index to the more significant aspects of the total environmental complex. Thus, the primary foredune zone, for example, is characterized by relatively high intensities of sand movement and salt spray deposition and low amounts of available soil moisture and ground water salinity. The several facets of a primary foredune—foreslope, top, and backslope—are all essentially xeric, but they differ considerably in regard to sand movement and salt spray intensity. Hollows in the primary and secondary backdune zones are characterized by large amounts of available soil moisture, small amounts of ground water salinity, and virtually no sand movement, but those near the shoreline receive more salt spray than those farther inland. As a final example, intertidal peat flats in the bayshore zone are characterized by low salt spray intensity, intermittent or catastrophic sand movement, and excessive amounts of saline water. Ground water salinity varies with the regimen of tidal flooding and rainfall and with microrelief.

TOLERANCE OF PLANTS TO SALT SPRAY

INTRODUCTION

The preceding study has established the existence and character of a salt spray gradient of decreasing and varying intensity from east to west across Island Beach. If the available species vary in their tolerance to salt spray, we should find these species occurring along the salt spray gradient in positions predetermined by their relative tolerances.

In order to test this hypothesis, it was necessary to devise some means of rating the available species according to their relative tolerance to salt spray. In attempting to obtain experimental data for this purpose, comparable to that obtained by Oosting (1945) for some of North Carolina's coastal species, it was assumed that the response exhibited by any given species to an artificial spray of sea water would be similar, in all essential respects, to its response to a natural spray of sea water.

Mid-summer was selected as the most advantageous time to conduct such an experiment in the field. At this time of year, almost all of the species it was deemed desirable to test are in aproximately the same stage of vegetative development. The early-flowering species, mostly woody, have completed their reproductive cycle; the late-flowering species, mostly herbaceous, have completed their vegetative growth; and all have mature foliage.

The period from mid-July to mid-August has the added advantage of a normally favorable weather regime. The weather actually experienced during this period in 1957 was free of any appreciable precipitation. There was no measurable rainfall, one day was foggy, and there were two days on which dew collected on plants in low, protected hollows. Winds were light and variable, not the sort that carry large amounts of salt spray, and temperatures were seasonable.

METHODS

Three specimens of each of 50 species were selected as experimental subjects. For woody species, the word "specimen" refers to a branch having 100 or more healthy leaves. For herbaceous species, it refers to a 1 sq m quadrat in a pure or nearly pure stand.

The species selected were chosen to provide examples of all or nearly all of the life-forms represented in the flora and all or nearly all of the major communities represented in the vegetation cover. Care was taken to select healthy specimens growing in sites where they would be protected from windborne salt spray. Each specimen was marked with a yellow, plastic tag to facilitate its location and identification.

Each specimen was subjected to 15 consecutive treatments with sea water. Each treatment consisted of thoroughly wetting the foliage with undiluted sea water applied as a fine mist from a standard garden spray apparatus. The sea water was collected from the surf and filtered immediately before use. Treatments were made daily between 8 a.m. and 12 noon from July 11 to July 26, 1957.

Beginning the second day, the amount of dead foliage (foliage burning) exhibited by each specimen was recorded daily. This was estimated as a percentage of the actual leaf area affected. Notes were also made as to discoloration other than burning, the part of the leaf first affected, the progression of burning, the comparative response of leaves with respect to their position on the branch or plant, differences in response between intact and insect damaged leaves, and apparent recovery which occurred as new growth following partial defoliation in a few species.

Each specimen was examined again on August 10—15 days after the last treatment (30 days after the first). At this time, the percentage of foliage burned, degree of recovery, and condition of buds were noted.

Averages were calculated and a graph was prepared for each species to show the rate of foliage burning, and, in a few cases, the degree of recovery after treatments were discontinued. The various species were then arranged in order of decreasing resistance (Table 13) to sea water according to the following criteria: (1) Species which exhibited no

detectable response were rated as having absolute resistance. (2) The remaining species were then arranged in increasing order of foliage burning exhibited 15 days after the last treatment. (3) Those exhibiting 100% foliage burning at that time were rearranged in increasing order of foliage burning exhibited at the time of the last treatment. (4) Species found to be alike in both these respects were rearranged according to the number of treatments applied before the first response was noted. (5) Thirteen species suffered 100% foliage burning before the last treatment was applied. These were arranged in two groups—one which showed no recovery and one which showed some recovery 15 days after the last treatment.

RESULTS

On the basis of the results obtained in this experiment, the species tested were rated and classified (Table 13) according to their relative resistance to treatments with seawater. Some species (Group A) showed no response to treatment, and are therefore considered to be completely tolerant to windborne salt spray. In other species, the foliage was 100% burned before the end of the treatment period. Some of these (Group F) showed no recuperation within 2 weeks after the treatments were discontinued. Others (Group G), in the same period of time, showed various degrees of recovery by new growth. The species between these two extremes exhibited an almost continually variable range of response from very little to almost complete foliage burning at the end of the treatment period. Some (Group B) showed little change after the treatments were discontinued, but others (Groups C, D, and E) continued to suffer injury and burning.

Except for the species in Group A, the first leaves to show evidence of burning were those which had been damaged mechanically or by insects. Burning of undamaged leaves did not usually appear until several days later. In most cases (as previously reported by Boyce 1954), burning appeared first at the tips of leaves and then proceeded along the margins and toward the mid-rib. The area around the mid-rib and near the base of the blade was the last to show the discoloration associated with burning. The fronds of *Osmunda regalis* and *O. cinnamomea* responded somewhat differently. Burning appeared first in leaflets near the acropetal end of the rachis and then proceeded basipetally down the rachis and peripherally along the leaflets. Leaflets of compound leaves (of angiosperms) reacted in much the same manner as simple leaves. Leaves of some species, e.g., *Rhus radicans* and *Parthenocissus quinquefolia*, became discolored, the former yellow and the latter red, before any signs of true burning appeared. The basal leaves of herbs such as *Hibiscus palustris* were affected before the terminal leaves, but often the terminal leaves were lost before the apparent damage was very great. Several other species, e.g., *Sassafras albidum* and *Vaccinium corymbosum*, became partly

TABLE 13. Response of mature foliage to 15 consecutive, daily applications of undiluted sea water. Species (except Group G) are listed in decreasing order of resistance to injury by sea water. Column 1—Number of days required for the first response to treatment, Column 2—Number of days required for 100% foliage burning, Column 3—Percentage of foliage burned at the time of the last treatment, Column 4—Percentage of foliage burned 15 days after the last treatment.

Group	Species	1	2	3	4
Group A:	*Ammophila breviligulata*	—	—	0	0
	Artemisia stelleriana	—	—	0	0
	Carex kobomugi	—	—	0	0
	Cakile edentula	—	—	0	0
	Iva frutescens	—	—	0	0
	Solidago sempervirens	—	—	0	0
	Spartina alterniflora	—	—	0	0
	Spartina patens	—	—	0	0
Group B:	*Ilex opaca*	13	—	5	5
	Panicum virgatum	12	—	7	7
	Juniperus virginiana	13	—	7	10
	Ilex glabra	14	—	10	10
	Baccharis halimifolia	11	—	15	15
	Typha latifolia	13	—	10	20
	Scirpus canadensis	10	—	20	20
	Vaccinium macrocarpon	14	—	10	25
	Phragmites communis	12	—	25	25
	Myrica pensylvanica	11	—	25	25
	Pinus rigida	10	—	20	35
	Convolvulus sepium	11	—	30	35
	Arctostaphylos uva-ursi	10	—	25	40
Group C:	*Amelanchier canadensis*	6	—	75	75
	Kalmia angustifolia	8	—	40	80
	Prunus serotina	5	—	70	90
Group D:	*Phytolacca americana*	8	>15	50	100
	Rhus copallina	7	>15	50	100
	Prunus maritima	6	>15	50	100
	Quercus ilicifolia	7	>15	55	100
Group E:	*Acer rubrum*	7	>15	70	100
	Vaccinium corymbosum	6	>15	70	100
	Hypericum virginicum	7	>15	75	100
	Smilax rotundifolia	6	>15	75	100
	Parthenocissus quinquefolia	6	>15	75	100
	Quercus marilandica	7	>15	85	100
	Quercus falcata	6	>15	85	100
	Hudsonia tomentosa	7	>15	90	100
	Lyonia mariana	5	>15	95	100
Group F:	*Osmunda regalis*	5	13	100	100
	Cyperus grayii	5	13	100	100
	Hibiscus palustris	4	11	100	100
	Dryopteris thelypteris	3	11	100	100
	Osmunda cinnamomea	5	10	100	100
	Euphorbia polygonifolia	5	9	100	100
	Polygonum articulata	4	8	100	100
Group G:	*Robinia pseudo-acacia*	4	11	100	20
	Viburnum dentatum	6	10	100	30
	Rhus radicans	6	14	100	70
	Sassafras albidum	6	14	100	80
	Rosa rugosa	5	13	100	80
	Rosa virginiana	5	10	100	90

or entirely defoliated before the apparent damage was very great. Several others, e.g., *Quercus ilicifolia* and *Q. marilandica*, retained their leaves long after they were completely dead.

Woody species exhibit a wide range of response patterns, but herbaceous species tend to exhibit an

all-or-nothing kind of response. Group A (Table 13), which shows absolute resistance, contains only one woody species; and Group F, which shows extremely low resistance, is composed entirely of herbaceous species. In other words, 14 of the 20 herbaceous species tested showed either absolute resistance or virtually no resistance at all, while the 30 woody species tested range from very high to very low resistance.

It is interesting to note that all the species in Group A (absolute resistance) are either xerophytes or halophytes. The species in Group B (very high resistance), with the exception of *Convolvulus sepium*, have small, xeromorphic, or graminoid leaves. All the species in Group F (very low resistance), except for *Cyperus grayii* and *Euphorbia polygonifolia* which are strict xerophytes, occur only on marshy sites and are presumed to be hydrophytes or mesophytes.

The examination of buds on August 10 revealed that most of the terminal and upper lateral buds of woody species were dead or appeared to be dead, but the lateral buds several nodes back from the apex appeared to be in good condition. (These observations were confirmed to be correct by a re-examination of many of the same specimens in May, 1958.) The lateral buds of the species listed in Group G became active immediately after defoliation and were definitely undamaged. Other woody species, e.g., *Prunus serotina* and *Myrica pensylvanica*, recover from natural salt spray damage in a different way. After the terminal and lateral buds of exposed twigs are killed by salt spray, new growth proceeds (during the following growing season) from adventitious buds which arise near the bases of dead twigs.

DISCUSSION

Boyce (1954) demonstrated that the heterotrophy of leaf tissue caused by exposure to salt spray does not occur until after the uptake of chloride ions. From this observation, he concluded that it is chiefly the chloride in sea water which causes salt spray injury. Consequently, it may be assumed that any factor which would tend to increase the amount of chloride absorbed by leaves should tend also to increase the amount of foliage burning.

Some of the factors to be considered in this respect are salt spray intensity and plant exposure, the efficiency of different kinds of plants as collectors of salt spray, precipitation, and atmospheric humidity. The factors having to do with the amount of salt spray deposited on plants in nature are effectively eliminated from consideration in the experiment described above. Test specimens were saturated with excessive amounts of undiluted sea water at each treatment. When sea water deposited on leaves either by natural or by artificial means has evaporated, the surfaces of the leaves are covered with thin films of salt crystals. Salt in this form is probably not very effective in causing injury, but it may become effective if converted to a solution. Any factor

which tends to increase the frequency or duration of instances when this film of salt is converted to a solution should tend to increase the rate of chloride uptake and hence the rate of foliage burning.

The leaves of test specimens in open sunlight on clear days rarely remained wet for more than an hour; but on two separate, overcast days, the leaves of test specimens (before treatment) were found to be moist while those of adjacent plants were quite dry. The adhering film of dry salt, having deliquescent properties, had absorbed enough moisture from the atmosphere to be converted to an adhering film of salt solution. Fog, dew, light rain, or drizzle could have the same effect as high humidity.

In the light of these considerations, the apparent correlation between resistance to sea water and xeromorphic leaf structure is not especially surprising. It seems reasonable to assume that structural features presumed to be effective in conserving moisture by preventing its loss from leaves might also be presumed to be effective in preventing the uptake of a salt solution.

The all-or-nothing response exhibited by most of the herbaceous species tested can also be explained, in part, by these considerations. All the resistant herbaceous species are succulent or graminoid xerophytes or halophytes. All but two of the non-resistant herbaceous species are broad-leaved mesomorphs. Except for the halophytic species, the plants in the resistant group were growing on dunes where their leaves dried rapidly and the bathing salt solution was renewed for only a short time each day. All the broad-leaved mesomorphs were growing in marshy habitats where the atmosphere surrounding them was undoubtedly more humid, especially at night, thus providing opportunities for the bathing salt solution to be renewed at frequent intervals and to persist for relatively long periods of time.

ECOLOGICAL IMPLICATIONS

It could be argued that the response of foliage to repeated applications of sea water is not a true measure of a plant's tolerance to windborne salt spray in nature. It could be argued, too, that the amount of salt recovered from bits of cheesecloth does not provide a true measure of the relative distribution of salt spray in nature. Nonetheless, the results of these two experiments provide the only quantitative basis for testing the following hypotheses: (1) Windborne salt spray is an important limiting factor in the environmental complex of Island Beach. (2) The relative intensity and amount of salt spray deposition—the distribution of salt spray—is controlled by topography; and therefore, salt spray gradients and salt spray distributional patterns are closely related to topographic patterns. (3) The available species differ in salt spray tolerance, and the arrangement of populations on the salt spray gradient is predetermined by the vagility and the ecological amplitude of each species' population in relation to the salt spray factor.

Many of the plant populations represented by the test specimens used in the experiment described above exhibit distributional patterns which conform nicely to the terms of these hypotheses. *Ammophila breviligulata*, *Artemisia stelleriana*, and *Cakile edentula*, for example, all given high resistance ratings, are most abundant on primary foredunes in the zone of extreme salt spray intensity. *Myrica pensylvanica*, given a high rating, is common in the forefront of Low Xeric Thickets bordering the Dunegrass zone, and it is found occasionally on the tops of primary foredunes. Similarly, *Ilex opaca* and *Juniperus virginiana* are often the tallest plants in the zone of high salt spray intensity. *Prunus serotina*, rated as moderately resistant, is most abundant on the landward slopes of secondary foredunes where, being in the wind shadow, it receives protection from salt laden winds. *Rhus copallina*, *Quercus marilandica*, and *Rosa rugosa*, all given lower resistance ratings, are found most commonly in well-protected habitats in the secondary backdune zone.

Another kind of situation is also apparent. Many of the species given a high resistance rating are rarely if ever encountered in the zone of high salt spray intensity. Some of these, e.g., *Iva frutescens* var. *oraria* and *Spartina alterniflora* are halophytes while others, e.g., *Baccharis halimifolia* and *Typha latifolia*, are hydrophytes capable of growing in brackish but not in highly saline situations. The zone of high salt spray incidence is also a xeric zone whose average surface elevation is well above that of the water table.

Some species rate low to extremely low in their resistance to damage by sea water, and yet they occur quite regularly in the zone of high to extremely high salt spray intensity. *Euphorbia polygonifolia*, *Rhus radicans*, *Parthenocissus quinquefolia*, and *Hudsonia tomentosa* are excellent examples of the case in point.

Euphorbia, for example, was given the second lowest resistance rating of all the herbaceous species tested. Yet, in contradiction to all expectations, it is restricted to areas of active sand movement in the zone of extreme salt spray intensity. It has been shown, however, that salt traps exposed 1 ft above the ground receive less salt spray than those exposed 3 ft above the ground. Traps which occasionally blew down and lay flat on top of the primary foredune were found to have received negligible salt spray deposits. Euphorbia, being a prostrate, spreading succulent and usually surrounded by Ammophila, has the same kind of exposure; and it actually receives very little if any salt spray.

The other species listed above are similarly favored by low growth-form. *Hudsonia tomentosa* is normally less than 1 ft high. *Parthenocissus quinquefolia* is a liana which, in the zone of high salt spray intensity, trails along the ground; and *Rhus radicans*, in the same kind of habitat, is a hardy shrub 1 to 2 ft in height. The latter has the added advantage of being able to recuperate rapidly (Table 13) by new growth from the lateral buds which escape injury by salt spray.

What about species of moderate resistance which occur in the intermediate zone of high to moderate salt spray intensity? *Ilex opaca* and *Juniperus virginiana*, for example, have received high resistance ratings; but when exposed to high salt spray intensity, Ilex assumes a salt-spray-molded growth-form like that described by Boyce (1954) for many woody species; and Juniperus, having a monopodial pattern of growth, is burned on the seaward side while the protected landward side remains green. (Most of the damage to Juniperus occurs during the winter months.) None of the woody species in either the shrubby or the arborescent zones are absolutely resistant to salt spray damage, but most of them can recuperate (by new growth) from minor injuries.

Shrubs along the exposed, seaward edge of a thicket community commonly exhibit salt-spray-molded growth-forms, and thus they form a canopy angle which varies in slope according to salt spray intensity. The plants in the center of such vegetation are protected from salt spray except at their tops. Evidence presented earlier (Table 12) suggests that the intensity of salt spray at canopy height is moderately high for a distance of 350 m or more from the ocean shoreline. Under such conditions (Fig. 10), terminal growth is suppressed by repeated salt spray injury to buds, and lateral growth is suppressed by crowding. Plants completely exposed to salt spray assume an "espaliered" shape (Boyce 1954), while those exposed only at the crown (Fig. 9) have a dense, flat-topped crown. Low Thickets (Figs. 4, 8) and High Thickets too (Figs. 9, 10), tend to have nearly level, nearly flat, and very dense canopies. In order for these thickets to grow in height, it is necessary that all the plants grow *en masse*. Faster growing or more resistant species may become emergent (Fig. 4), but they are eventually killed back to a level at which they receive the benefits of mutual protection.

The general conclusions to be derived from these several lines of evidence concerning the role of salt spray as a limiting factor may be summarized as follows: (1) In the zone of extreme intensity, salt spray exerts a selective effect. Species with absolute tolerance are definitely favored, but some species with low tolerance but a low growth-form adapted to escaping high salt spray intensity can also survive. (2) In the zone of high to moderate intensity, the effect of salt spray is to favor low growth-forms and to limit the height of potentially taller but less resistant growth-forms by suppressing terminal growth. (3) In the zone of lower to negligible intensity, the effects of salt spray are much less striking. The herbs and shrubs of the marsh zone, with the exception of *Acer rubrum* which is quite susceptible to salt spray injury, do not appear to be influenced in their growth-form by salt spray. Many of the taller trees in the arborescent zone, especially those which are open grown, have rounded, flattened, or de-

formed crowns (Figs. 13, 14) which appear to reflect the influence of salt spray.

The significance of salt air (air containing suspended droplets of sea water or particles of salt) as opposed to salt spray (which is deposited by impact on the seaward surfaces of plants) has not been studied and is not known. The kinds of arborescent vegetation described for Island Beach do not appear to occur anywhere on the mainland even though there are numerous habitats in which environmental conditions appear to be equivalent, except for the salt air, and the same species are present in the available flora. This situation suggests that salt air and small amounts of salt spray exert a controlling influence on arborescent as well as herbaceous and shrubby maritime vegetation, but the mechanism of this control is not readily apparent.

THE VEGETATION-ENVIRONMENT SYSTEM

GENERAL CONSIDERATIONS

Billings (1952) states that "The complexity of the interrelationship between the plant and its environment and between various factors of the environment is almost enough to discourage any attempts at a complete analysis and synthesis." He defines "the environment of a plant . . . as the sum of all external forces and substances affecting the growth, structure, and reproduction of that plant," and he goes on to say that ". . . the environment-plant system is a dynamic unit in itself and reacts as a whole."

Bray & Curtis (1957) sum up their view of environment-plant systems by pointing out that "There is . . . no simple cause and effect relationship between physical phenomena (as primarily causal) and biotic phenomena (as primarily effectual), especially in the more complex environments. There is, rather, instead of a domain which is determined by a small number of independent factors (that is, a system of mechanistic causality), a field of interrelated units and events (configurational causality)."

It is possible to recognize two fundamental approaches to the interpretation of plant-environment or vegetation-environment systems: (a) through a synthesis based on comprehensive environmental and autecological analyses, and (b) through a synthesis based on comprehensive vegetational analyses. Some of the methods used in the former approach are reviewed by Billings (1952), and some of those used in the latter are reviewed by Bray & Curtis (1957).

Both approaches require an expression of the distribution of species' populations along environmental gradients. Both approaches recognize that: (a) each plant species is distributed according to its own ecological valence (genetically determined physiological capacity) and its own vagility (ability to reproduce and migrate), and (b) the behavior of plants, individually or collectively in communities, represents a complex of responses to total environment. The environment-centered approach (as exemplified by Whittaker 1956) works from one side and the vegetation-centered approach (as exemplified by Curtis &

McIntosh 1951) works from the other side of this relationship. In this study of Island Beach, a small, preliminary attempt has been made to coordinate both approaches.

Much of the detailed information necessary for a truly comprehensive ecological perspective is not available at this time nor will it be readily available in the near future. Practical considerations have made it necessary or desirable to rely on those features of the vegetation and of the environment which are readily observable or conveniently measurable. Accordingly, the vegetation pattern has been described and its units classified on the basis of simple structural, compositional, and environmental characteristics. The environmental pattern has been decribed in terms of topography, physiographic processes, and a few significant limiting factors which are subject to topographic control. Topography has thus assumed a pivotal position in the description and tentative analysis of these patterns.

COMMUNITY-FACET RELATIONSHIPS

Specific interrelations among the topographic profile which characterizes the topographic pattern, the limiting factor gradients which characterize the environmental pattern, and the distribution of community types which characterizes the vegetation pattern of Island Beach are diagrammed in Figure 19. The central part of the chart shows a composite topographic profile and indicates the major topographic zones and landforms. The upper part shows the amount or intensity of salt spray, sand movement, soil moisture, and soil salinity. The lower part shows the principal habitat ranges of community types which are considered to be representative of pioneer, intermediate, and terminal stages in the xerosere, hydrosere, and halosere.

In general, the amount of salt spray and sand movement decreases from east to west (left to right on the chart) while the amount of soil moisture and soil salinity increases. Variations in these general trends are associated with variations in the topographic profile. Each topographic facet is seen to have a somewhat different combination of limiting factor intensities. The top of a primary foredune, for example, is characterized by very large amounts of salt spray and sand movement but very small amounts of soil moisture and soil salinity. A hollow in the area of secondary backdunes is characterized by moderate (usually negligible but occasionally significant) amounts of salt spray, sand movement, and soil salinity and a very large amount of soil moisture.

Most of the community types recognized on Island Beach are associated with one or a few kinds of topographic facets. Some community types, e.g., Fresh Marsh and Salt Marsh, occur only on one kind of facet. Some facets, e.g., the tops of primary foredunes and intertidal peat flats (see outer bayshore zone), support only one kind of plant community. Between these two extremes, and much more common, are the kinds of topographic facets that can support
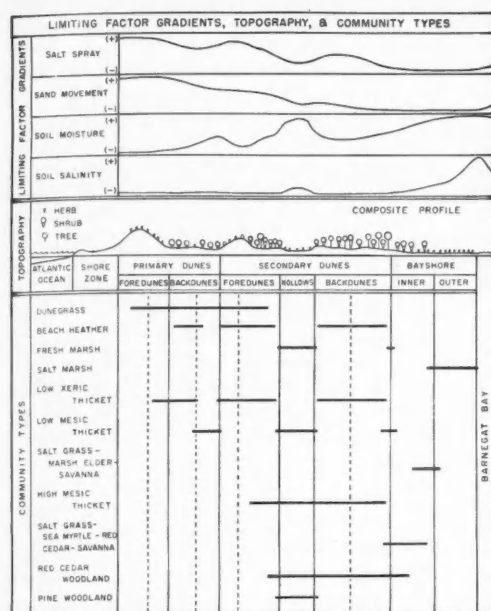
FIG. 19. The interrelation of topography, limiting factor gradients, and community types. (+) indicates increasing and (−) indicates decreasing amounts or intensities of the limiting factors. The bars opposite the names of community types indicate their principal habitat ranges.

more than one community type and the community types that can occur on more than one kind of facet.

In general, community-facet relationships are inherent in the definition of a plant community as an aggregation of plants having uniformity of structure and composition and occupying an area of more or less uniform environmental conditions. Since each facet is characterized by a different combination of limiting factor intensities, the general community-facet relationship has a basis in the topographic control of limiting factor gradients.

Reciprocal community-facet relationships such as that between Dunegrass communities and primary foredunes and that between Salt Marsh communities and intertidal peat flats are characteristic of environmental extremes and have a twofold basis— partly biotic and partly physical. The continued existence of both the community and the facet depends on the continuing modification of physical forces by biotic forces. Under these conditions, plant succession without physiographic change is virtually impossible. Dunegrass communities on the back-slopes of primary foredunes may be replaced or cornered by the encroachment of Low Xeric Thicket; but, in the absence of aggressive woody species which are able to withstand high intensities of salt spray and sand movement, it is not likely that Dunegrass will be replaced on the tops of these dunes. Succession in the halosere from Salt Marsh to Salt Grass-Marsh

Elder Savanna or to Salt Grass-Sea Myrtle-Red Cedar Savanna or to Brackish Marsh and the Brackish Marsh seral communities appears to be initiated only by physiographic causes and directed perhaps by environmental changes such as decreases in ground water salinity over which the vegetation has little if any direct control or influence.

Most of the community-facet relationships in the vegetation of Island Beach are nonreciprocal, i.e., most community types can occur on more than one kind of facet and most kinds of facets can support more than one community type. (This consideration does not alter the specific community-facet relationship between individual plant communities and individual topographic facets.) These nonreciprocal community-facet relationships probably indicate successional relationships. The probable successional sequence on a particular kind of facet can be interpolated in part from Figure 19 by reading down each column (lower part of chart) from top to bottom. The pioneer or initial community in a protected hollow in the area of secondary backdunes, for example, may be Fresh Marsh which may be replaced successively by Low Mesic Thicket, High Mesic Thicket, and Red Cedar or Pine Woodland.

SUCCESSIONAL RELATIONSHIPS

In the absence of long-term data relating to succession, we must rely on these nonreciprocal community-facet relationships and on the structural and compositional characteristics of the vegetation to provide clues to probable successional relationships.

In the more mesic parts of the primary backdune area, Dunegrass appears to be the pioneer community. (There is evidence in a few areas that Cranberry Bogs or Fresh Marshes might play a pioneer role in areas of exceptionally low elevation.) Where Dunegrass is pioneer, the intermediate stage is probably a Dunegrass-Shrub Savanna (Fig. 11) or a Dunegrass-Low Thicket Mixture. The terminal stage may be either a Low Xeric Thicket or a Low Mesic Thicket depending on the amount of sand deposited during the early and intermediate stages of vegetational development.

On the more xeric parts of both the primary and the secondary dune zones, the major pioneer stage is represented by Beach Heather communities. This stage appears to be long persistent on some facets, e.g., the seaward slopes of secondary foredunes, and on secondary backdunes of higher than usual elevation. In other places it seems to be replaced by various Beach Heather-Thicket Mixtures. The terminal stage of the xerarch succession appears to be Low Xeric Thicket in the primary backdune area, the zone of high salt spray intensity, and Low Dune Thicket on the tops of secondary foredunes. In the secondary backdune zone, the zone of moderate salt spray intensity, the terminal stage may vary from High Dune Thicket to Red Cedar Woodland.

The pioneer communities of hydrarch succession in depressions and on low flats in the secondary backdune zone are various kinds of Fresh Marsh commu-

nities. The intermediate stages in this sere are Fresh
Marsh-Marsh Thicket Mixtures and Low Marsh
Thicket or Low Mesic Thicket. High Marsh Thicket
and Swampy Red Cedar Woodland which seem to
qualify as subterminal and terminal stages are rare.
Evidence of physiographic succession initiated by the
accumulation of sand on Fresh Marshes is incon-
clusive. Only one place was found in which a deposit
of peat under a layer of sand could be identified as
fresh marsh peat, but it is likely that many areas
now occupied by Low Mesic Thicket or High Mesic
Thicket were once marshy in character.

The successional trends associated with the bay-
shore topographic zone are even more varied. Salt
Marsh succession resulting in the kind of zonation
encountered on transect VI (Fig. 17) has already
been described. Succession on ice-pushed sand ridges
is relatively easy to interpret. Pioneer Reedgrass
communities are eventually replaced by Reedgrass-
Sea Myrtle and Reedgrass-Sea Myrtle-Red Cedar
Mixtures. Salt Marshes which are removed from tidal
influences by the formation of sand ridges become
brackish or fresh and undergo various successional
changes. Fresh Marsh elements usually play some
part, and *Baccharis halimifolia* (sea myrtle) is fre-
quently the dominant shrub in the later stages.

Dunegrass and Salt Marsh communities are es-
sentially stable. In the zone of high but not extreme
salt spray and in the zone of moderately high ground
water salinity, biotic succession can occur; but it is
inhibited; and the terminal or long-persistent sub-
terminal stages are Low Thickets: Low Xeric or Low
Mesic Thickets in the former and Salt Grass-Marsh
Elder Savanna or Brackish Marsh-Sea Myrtle Mix-
tures in the latter. In the mesic zone, where the in-
tensity of salt spray, sand movement, and ground
water salinity are non-limiting, and moisture condi-
tions are at their presumed optimum, biotic succes-
sion is not so inhibited. The highest (tallest and
successionally most advanced) plant communities
present on Island Beach are Red Cedar Woodland
and Pine Woodland, but their designation as true
salt spray climax is open to some doubt. The sap-
lings under Red Cedar Woodland are mostly *Ilex
opaca*, and the saplings under Pine Woodland are
mostly *Chamaecyparis thyoides*. Furthermore, there
are very few favorable habitats available for the de-
velopment of these communities, and cornering rather
than effusion is the rule for arborescent vegetation
in general.

All of the important species in these two kinds of
woodland communities can be found on the adjacent
mainland and in other maritime areas. There are a
few areas on the mainland farther north (Kelly 1927),
at Sandy Hook (Chrysler 1930) and on Long Island
(Svensen 1936) which bear a superficial resemblance
to the Pine Woodland communities on Island Beach.
The structural and compositional character of the
Pine Woodland area (Fig. 2:2.5-3.5) of Island Beach
does not seem to be duplicated, however, anywhere
on the mainland or on the strand. Likewise, the

species present in the Red Cedar Woodland com-
munities described earlier are also present on the ad-
jacent mainland and in maritime areas to the south
(Snow 1902, Chrysler 1910) and to the north (Chrys-
ler 1930, Conard 1935). Red Cedar Woodland com-
munities having the same structure and composition
of those on Island Beach are not, however (to the
author's knowledge), duplicated anywhere else. Per-
haps one or both of these woodland communities is
a true salt spray climax, but the evidence and data
necessary to formulate a more precise interpretation
are not presently available.

Topographic changes and concomitant vegetational
changes are characteristic features of this vegetation-
environment system. Changes are especially frequent
in the primary dune zone at the northern end of the
park area, and in parts of the bayshore zone near the
inlet. Between the primary foredunes and the bay-
shore zone, the processes of change are slower and
less dramatic but still apparent.

In its broader aspects, plant succession on Island
Beach is controlled by oscillations in the interaction
between physical and biotic forces. A more precise
description of successional patterns must necessarily
await the accumulation of more precise data con-
cerning the environmental and vegetational processes
involved. Even at this stage of knowledge, however,
it seems reasonable to conclude that plant succession
on Island Beach, and perhaps on barrier beaches in
general, is largely an interzonal phenomenon. The
herbaceous, shrubby, and arborescent zones do not
necessarily represent seral stages in biotic (autogenic)
succession. The herbaceous zones (Dunegrass and
Salt Marsh) are structurally and compositionally
stable under the environmental conditions which char-
acterize them. Within the environmentally less se-
vere shrubby and arborescent zones, several sere—
xerosere, hydrosere, and halosere—are recognizable,
and the structure of terminal stages is determined
by environmental limitations—especially salt spray
intensity.

SUMMARY

1. Island Beach State Park occupies a 10-mile
stretch of barrier beach on the coast of New Jersey.
The natural vegetation and environment of this area
are extremely diversified.

2. The vegetation pattern depicted by a detailed
vegetation map is a zoned mosaic. The herbaceous
zone, on the east, is relatively uniform and made up
almost entirely of Dunegrass communities. The
shrubby, arborescent, and marsh zones, on the other
hand, are complex mosaics composed of numerous in-
dividual plant communities which vary greatly in
size, structure, composition, and habitat.

3. The topographic pattern is also a zoned mosaic.
The shore zone, shaped by the action of waves and
wind, is relatively uniform in configuration. The
primary and secondary dune zones and the bayshore
zone, arranged in order from east to west, are topo-
graphically diversified. Each topographic zone is

represented by a different mosaic of landforms and topographic facets. The physiographic processes responsible for this topographic configuration result from the interaction and oscillation of physical forces and biotic forces. The process of dune-building, for example, requires the integrated action of waves, winds, and Dunegrass communities.

4. The relationship between vegetational and topographic patterns is such that individual plant communities tend to be coextensive with topographic facets. Some community-facet relationships are reciprocal, i.e., certain kinds of facets support only one kind of plant community. Others are non-reciprocal, i.e., some kinds of facets support several different kinds of plant communities. Reciprocal community-facet relations indicate environmental and vegetational stability while non-reciprocal relations indicate probable successional trends and relationships.

5. That topography is the major controlling factor in this environmental complex was illustrated by measuring the intensity or amount of sand movement, available soil moisture, ground water salinity, and salt spray deposition in relation to the topographic profile. The topographic control of these limiting factor gradients is such that each zone, and the different facets within each zone, are characterized by a different combination of environmental conditions. Each topographic facet is an area of more or less uniform environment and therefore constitutes a distinct habitat. In this fashion, topography serves as an index to significant differences in the total environmental complex.

6. On the basis of evidence derived from vegetational and environmental analyses, the zoned mosaic pattern of vegetation on Island Beach is interpreted as representing the summation of plant responses to an environmental pattern of similar design. Under the control of topography, this environmental pattern has the same general outlines as the zoned mosaic pattern of topography.

7. A study of species distribution in relation to salt spray tolerance (determined by experiment) and the salt spray gradient (determined by measurement) suggested the general conclusion that: Salt spray intensity, not biotic (autogenic) succession, is the factor largely responsible for the existence of herbaceous, shrubby, and arborescent vegetation zones on Island Beach arranged in order from east to west. The marsh zone is related to tidal action and ground water salinity.

8. Topographic, environmental, and vegetational patterns are clearly interrelated and interacting. In the main line of this interaction, topography controls the environmental gradients and patterns to which vegetation responds. Interactions of a lesser magnitude include the influence of vegetation and environment on topography and the influence of vegetation on environment. The result of these three-way interactions is a complex vegetation-environment system which exists and responds as a whole.

9. Successional trends and relationships, inferred from compositional and structural similarites or dissimilarities among plant communities and from the numerous nonreciprocal community-facet correlations, suggest that succession on Island Beach is largely an interzonal phenomenon. High salt spray intensity, high ground water salinity, high water table, and deficient amounts of available soil moisture tend to inhibit autogenic succession. Thus, the pioneer communities in the most extreme habitats of each vegetation zone are either stable or long persistent. Salt spray is especially important in this respect; for, even in the more mesic habitats, it tends to inhibit autogenic succession by suppressing the terminal growth of shrubs and trees.

LITERATURE CITED

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. 27: 251-265.

Boyce, S. G. 1954. The salt spray community. Ecol. Monog. 24: 29-67.

Bray, J. R. & J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monog. 27: 325-349.

Chrysler, M. A. 1910. The ecological plant geography of Maryland: coastal zone, western shore district. Vol. 3, Maryland Weather Service.

———. 1930. The origin and development of the vegetation of Sandy Hook, New Jersey. Torrey Bot. Club Bull. 57: 163-176

Conard, H. S. 1935. The plant associations of central Long Island. Amer. Midland Nat. 16: 433-516.

Curtis, J. T. & R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Dansereau, P. 1956. Le coincement, un processus écologique. Acta Biotheoretica 11: 157-178.

———. 1957. Biogeography. New York: Ronald Press. 394 pp.

Davis, J. H. 1957. Dune formation and stabilization by vegetation and plantings. Tech. Memo. No. 101. Beach Erosion Board, Corps of Engineers, Department of the Army.

Fernald, M. L. 1950. Gray's Manual of Botany. 8th ed. New York: American Book Co. 1632 pp.

Harshberger, J. W. 1900. An ecological study of the New Jersey strand flora. Acad. Nat. Sci. Phila. Proc. 1900: 623-671.

Johnson, D. W. 1919. Shore processes and shoreline development. New York: Wiley. 524 pp.

Kelly, A. P. 1927. Dune formation by pine barren plants. Bot. Gaz. 83: 89-93.

Knight, J. B. 1934. A salt-marsh study. Amer. Jour. Sci. 28: 161-181.

Lucke, J. B. 1934. A study of Barnegat Inlet, New Jersey and related shoreline phenomena. Shore & Beach Journal. 2: (April). (2), April, 1934.

Miller, W. R. & F. E. Egler. 1950. Vegetation of the Wequetequock-Paweatuck tidal-marshes, Connecticut. Ecol. Monog. 20: 143-172.

Moul, E. T. & R. W. Brown. 1957. Nonalgal marine

plants. Geol. Soc. Amer. Memoir **67** (Vol. 1): 1051-1058.

Oosting, H. J. 1945. Tolerance to salt spray of plants of coastal dunes. Ecology **26**: 85-89.

——. 1954. Ecological processes and vegetation of the maritime strand in the southeastern United States. Bot. Rev. **20**: 226-262.

——. 1956. The Study of Plant Communities. 2nd. ed. San Francisco: W. H. Freeman & Co. 440 pp.

Oosting, H. J. & W. D. Billings. 1942. Factors effecting vegetational zonation on coastal dunes. Ecology **23**: 131-142.

Small, J. A. 1945. Minutes of the meeting of March 21, 1945. Torreya **45**: 59-61.

——. 1954. Species reported from Island Beach, New Jersey. 9 pp. (mimeo.).

——. 1954. **Carex kobomugi** at Island Beach, New Jersey. Ecology **32**: 289-291.

Small, J. A. & W. E. Martin. 1958. A partially annotated catalogue of vascular plants reported from Island Beach State Park, New Jersey. Torrey Bot. Club. Bull. **85**: 368-377.

Snow, L. M. 1902. The ecology of the Delaware coast. Bot. Gaz. **34**: 284-306.

Svensen, H. J. 1936. The early vegetation of Long Island. Brooklyn Bot. Gard. Record **25**: 207-227.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monog. **26**: 1-80.

Woods Hole Oceanographic Institution. 1946. The determination of chlorinity by the Knudsen Method. Woods Hole, Massachusetts. 22 pp.

THE ECOLOGY OF *CONUS* IN HAWAII[*]

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TABLE OF CONTENTS

INTRODUCTION

Members of the gastropod genus *Conus* (Prosobranchia: Conidae) are among the most conspicuous invertebrates on the coral reefs and marine benches that fringe the Hawaiian Islands. At least 21 species of *Conus* are known to occur in these habitats.

Investigation of these natural populations was stimulated by the existence of such a large number of closely related species in a restricted environment. This phenomenon is not unique to *Conus*, for many other genera of marine invertebrates are also characterized by large numbers of sympatric species in tropical regions. The gastropod genera *Cypraea*, *Mitra*, and *Terebra* are represented by 30-50 species in Hawaii (Edmondson 1946). A non-molluscan example is the snapping shrimp genus *Alpheus*, represented by 30 species in Hawaii (Banner 1953). The evolution of such genera has contributed to a marked enrichment of the tropical littoral epifauna. Here the number of species approaches ten times that of temperate regions (Thorson 1956).

Although these assemblages are well-known to systematists, no previous comparative ecological studies are known to the present writer. The objective of the study reported here was to describe the ecological niches of the species, to determine the extent of isolation between ecologically similar species, and thus to elucidate the mechanisms that permit a large number of closely related species to survive and retain their identity in a narrow environment.

This paper is the first in a projected series reporting the results of ecological observations on natural populations of *Conus* in different areas, with emphasis on the Indo-West Pacific region. The research reported here was carried out while the author was a fellow of the National Science Foundation. Financial aid was also received from the Higgins Fund and the Director's Fund, Sheffield Scientific School.

of the figures is gratefully acknowledged. The author
is especially grateful to Dr. Olga Hartman for identi-
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food and feeding. Without her willing and patient
attention to a collection of partly digested, frag-
mentary remains of polychaetes, the food analyses
presented here would not have been possible.

THE GENUS *CONUS* IN HAWAII

Of 45 species of *Conus* previously reported from
the Hawaiian area, 32 are known from two or more
specimens collected alive and are thus considered to
be valid constituents of the Hawaiian marine fauna.
Ecological observations on 25 of these, listed below,
will be reported in this paper. Eighteen species were
collected by the writer in the subtidal coral reef
(noted by *) and intertidal marine bench (noted
by +) habitats to be discussed in detail below, The
specific names used are those given by Kohn (1959).

> *Conus abbreviatus* Reeve*+
> *Conus catus* Hwass *in* Bruguière+
> *Conus chaldaeus* (Röding)*+
> *Conus distans* Hwass *in* Bruguière*+
> *Conus ebraeus* Linné*+
> *Conus flavidus* Lamarck*+
> *Conus imperialis* Linné*
> *Conus leopardus* (Röding)
> *Conus lividus* Hwass *in* Bruguière*+
> *Conus marmoreus* Linné*
> *Conus miles* Linné*+
> *Conus moreleti* Crosse
> *Conus nussatella* Linné
> *Conus obscurus* Sowerby
> *Conus pennaceus* Born*+ (Fig. 1)
> *Conus pertusus* Hwass *in* Bruguière
> *Conus pulicarius* Hwass *in* Bruguière
> *Conus quercinus* Solander
> *Conus rattus* Hwass *in* Bruguière*+
> *Conus retifer* Menke+
> *Conus sponsalis* Hwass *in* Bruguière*+
> *Conus striatus* Linné*
> *Conus textile* Linné
> *Conus vexillum* Gmelin*+
> *Conus vitulinus* Hwass *in* Bruguière*

Most of the species listed are widely distributed
throughout the Indo-West Pacific region. One spe-
cies, *Conus abbreviatus*, is believed to be endemic to
the Hawaiian archipelago. It is closely related to
Conus coronatus Gmelin, which occurs in other areas
of the central and western Pacific.

Conus nanus Broderip is here regarded as con-
specific with *C. sponsalis*, but the Hawaiian popula-
tions probably constitute a valid subspecies. All
specimens of *C. marmoreus* known from Hawaii
agree with the description of *C. bandanus* Hwass *in*
Bruguière. Most systematists consider the latter a
variety of *C. marmoreus*, but the Hawaiian popula-
tions probably constitute a valid subspecies.

THE HABITAT OF *CONUS*

Marine benthic communities may be separated
into two principal types, "those that tolerate or re-
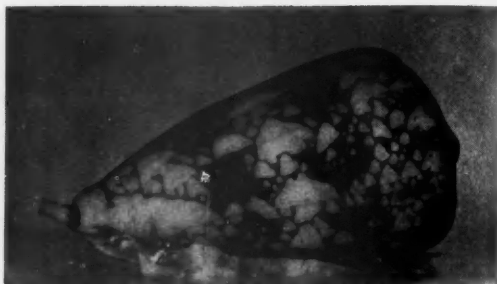

FIG. 1. Photograph of *Conus pennaceus* Born. Length
of shell about 35 mm. Photograph by C. E. Cutress.

quire exposure to the atmosphere and occupy stable
and usually hard substrata exposed to the full force
of the air with each important fall of tide," and
"those that do not tolerate exposure to the atmosphere
and are practically always submerged in water"
(Clements & Shelford 1939: 323).

The present paper deals primarily with the ecology
of natural populations of *Conus* which occupy hab-
itats of these two types, marine benches and coral
reef platforms, respectively. Notes on species occu-
pying other habitats will also be included.

THE MARINE BENCH HABITAT

The geomorphology of emerged marine benches in
the Hawaiian Islands has been discussed in detail by
Wentworth (1938, 1939). These benches result from
the single or combined action of processes designated
by Wentworth as solution benching, water-level
weathering, ramp abrasion, and wave quarrying.

SOLUTION BENCHES

In the Hawaiian Islands, solution benches occur
where the shoreline is composed of reef rock and
calcareous sandstone. On Oahu, this type of shore
comprises 52 miles, or 31% of the coastline (Went-
worth 1938). A detailed description of the charac-
teristics and formation of solution benches is given
by Wentworth (1939). A typical shore profile is
shown in Fig. 2A.

Unbroken units of bench are ordinarily a few
hundred feet long and 5-70 ft in width. The bench
platforms are very flat. "The normal bench surface
commonly shows variations of elevation of not over
three to six inches in an area fifty feet wide by one
hundred feet in length." (Wentworth 1939.) The
outer edge of the solution bench rises more or less
steeply from the water. The bench surface is ordinar-
ily a few inches to 3 ft above mean sea level, and
there is no raised rampart at the seaward margin.
The bench itself is usually reef limestone, which
consists of the firmly lithified skeletons of coral and
calcareous algae. On the sloping outer edge, cal-
careous algae and, to a lesser extent, corals, contrib-
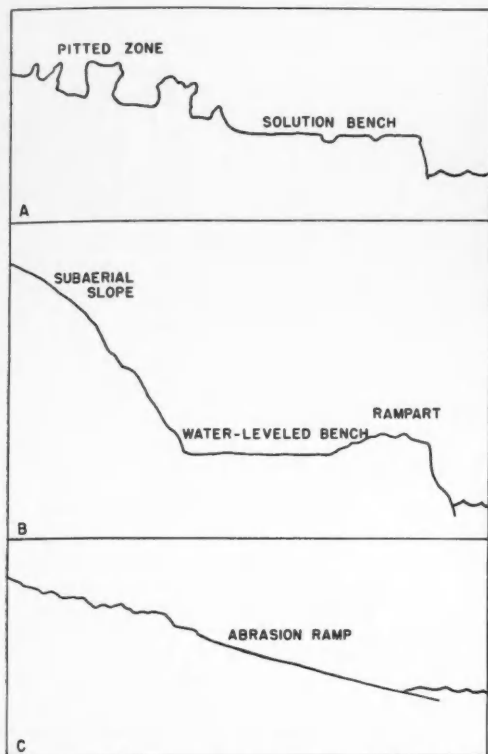ute active building of the bench out from shore.

FIG. 2. Profiles of Hawaiian marine benches. A. solution bench. B. Water-leveled bench. C. Abrasion ramp bench. Modified from Wentworth (1938, 1939).

FIG. 3. Photograph of solution bench at Kahuku, Oahu (Station 5). The width of the bench (left to right) is about 60 ft. The seaward margin of the zone of pitted limestone is visible at the left.

Other organisms, chiefly echinoids, are a destructive force in the same region.

The shoreward edge of the bench is sharply delimited by the front of a zone of pitted limestone (Fig. 3), ordinarily 10-50 ft in width and rising to a height of one to several ft above the bench surface. Wentworth (1939) presents evidence to show that this type of bench is formed chiefly by dissolution of the shoreward zone of pitted limestone by rain water, which collects in its pools; wave quarrying may finally produce the flat surface.

Details of solution benches selected for study are as follows:

Kahuku, Oahu (Sta. 5). The solution bench at Kahuku (Figs. 3, 4) is typical of the formation and was thoroughly investigated. It extends for several hundred feet along shore and is 40-80 ft wide. The bench surface is about one foot above mean sea level and is completely exposed for periods of up to four hours at tides of +0.2 feet[1] or less when seas are fairly calm. The coast here is exposed, and trade winds are ordinarily quite strong (about force 5). At high tide, the bench is strongly awash, and observations on it are not possible. The bench platform,

[1] All tidal data are referred to O datum = mean lower low water and are from Coast and Geodetic Survey Tide Tables.

which is of solid reef limestone with a few potholes, is covered by a well developed algal turf. Zonation of algae across the bench is present. The landward portion is characterized by *Laurencia* sp., *Sargassum polyphyllum* J. Agardh, and *Microdictyon setchellianum* Howe; the central portion, by *S. polyphyllum*, *S. echinocarpum* J. Agardh, and *Halimeda discoidea*, Decaisne; and the seaward portion, by *S. echinocarpum*, *H. discoidea* and *Dictyosphaeria cavernosa* (Forskäl) Børgesen. *Lyngbya majuscula* Harvey ex Gomont and *Cladophoropsis membranacea* (C. Agardh) Børgesen are also of common occurrence.

Nanakuli, Oahu (Sta. 11). On the leeward coast of Oahu, a limestone shore with solution benches extends, with interruptions, from Nanakuli Beach to the northern end of Nanakuli town, near Maile Head (Fig. 4). The bench is generally 50 ft or less wide, although at the end of one section it is about 100 ft. This is a very short section, however, and the bench there occupies less than one-half acre. The bench platform is about one foot above sea level, but it is less often exposed than is the bench at Station 5, described above. This is due to a prevailing heavy swell in the region, so that even at low tide large waves breaking over the bench may make collecting impossible. The algal turf is as well developed here as at Station 5. *Valonia aegagropila* C. Agardh is the dominant species. *Jania capillacea* Harvey, *Sargassum* sp., and *Padina* sp. are common. Zonation of algae was not studied, but it was not obvious.

Gastropods other than *Conus* common on solution benches are *Mitra litterata* Lamarck, *Haminoea aperta* Pease, and *Cypraea caputserpentis* Linné. A number of sea anemones are abundant. The most conspicuous Crustacea are xanthid crabs, snapping shrimp, and hermit crabs. The microfauna is especially rich. Prominent are amphipods, isopods, harpacticoid copepods, polychaetes, and Foraminifera.

WATER-LEVELED BENCHES

A formation typical of palagonite tuff and weathered basalt shores in Hawaii is the water-leveled bench, the characteristics and origin of which are dis-

cussed in detail by Wentworth (1938). Benches of this type may be 10-12 ft above sea level on exposed coasts, but are only 2-3 ft above sea level in sheltered places. Most of them are less than 100 ft wide. A steep subaerial slope landward of the bench is characteristic (Fig. 2B).
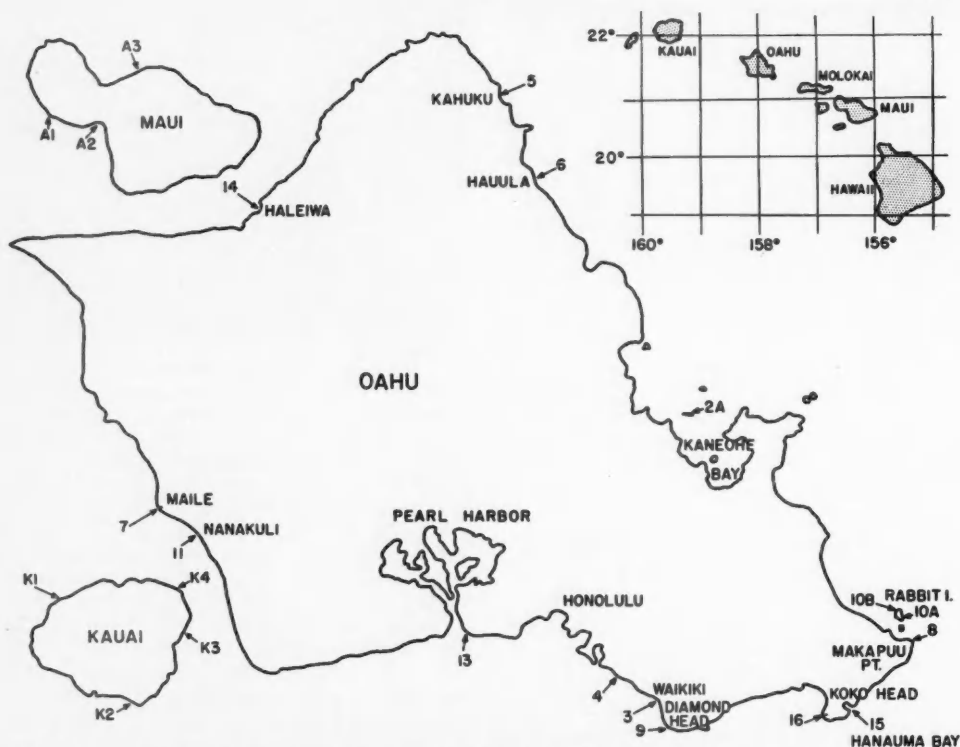
Unlike the solution bench, water-leveled benches are characterized by a well-developed rampart (Fig. 2B) of slightly higher rock at the seaward edge. The outer face of this zone is a steep cliff, characteristically occupied by echinoids. Landward of the rampart is the water-leveled bench proper. Its surface may be quite smooth or bear vertical irregularities of the order of a few inches to a foot. These are often due to differences in hardness of the dipping beds of tuff on which this type of bench is most often found.

Water-leveled benches which were given special study were as follows:

Lower Paia, Maui (Sta. A3). A fairly typical water-leveled bench near Lower Paia, Maui (Figs. 4, 5) was visited on 5 August 1956. The shore profile at this station is similar to that shown in Fig. 2B. The seaward face of the rampart zone is steep. The rampart zone (Fig. 5) averages about 15 ft wide. Its surface is irregular and is covered by a luxuriant algal turf, composed of many species. The water-

FIG. 5. Photograph of water-leveled bench at Lower Paia, Maui (Station A3) from subaerial slope. The 100-sq ft quadrat is outlined. Tide pools and rampart are also visible.

leveled part of the bench (Figs. 2B, 5) is about 15 ft wide and quite smooth. It bears a low algal turf which binds some sand. The tide was extremely low (−0.2 ft) during the period of observation, and this region was quite dry. Landward of it are large tide pools 1-2 ft deep (Fig. 5).

Milolii, Kauai (Sta. K1). Two broad marine

FIG. 6. Outline map of the south shore of Oahu, showing the nearly continuous fringing reef, Stations 3, 4, and 9, and landmarks.

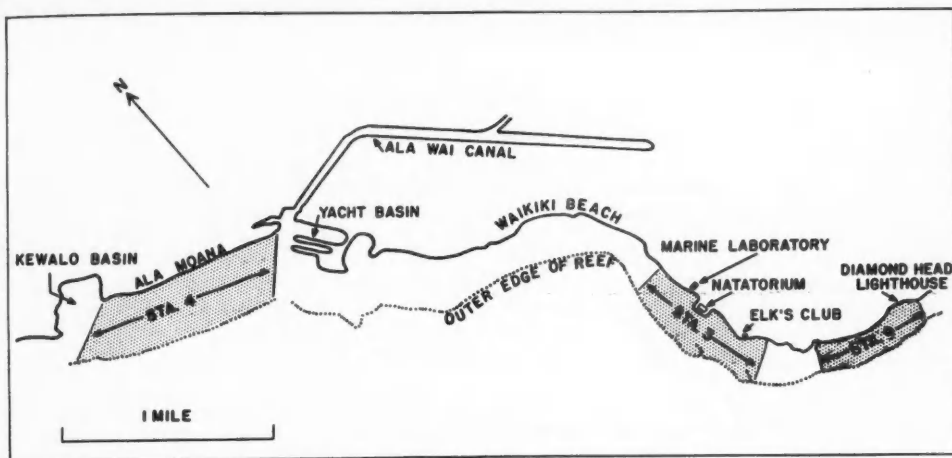benches fringe the shore at each end of a small beach, just east of Milolii Valley on the Napali (north) coast of the island of Kauai (Fig. 4). This region is accessible only from the sea. Four days were spent in the area in August 1955. The surface of the bench studied is about one foot above mean sea level. At minus tides it is completely exposed to the air. The benches reach a maximum width of about 200 ft. The algal turf of the platform is very low and does not present a "healthy" appearance. The dominant species is *Wurdemannia miniata* (Lamarck and DeCandolle) Feldmann and Hamel. Other species observed were *Dictyosphaeria* sp., probably young *D. cavernosa* (Forskål) Børgesen, *Gelidiella* sp., *Jania capillacea*, and *Valonia aegagropila*. At about 110 ft from shore a low pink encrusting alga, probably *Porolithon* sp., is present, and it continues to the seaward edge. The differences in flora between Station K1 and the solution benches may be due to the absence of heavy surf over most of the former.

ABRASION RAMP BENCHES

The distribution and formation of abrasion ramp benches on Hawaiian shores has not been treated in detail, but Wentworth (1938) includes a photograph of one. The formation is found on limestone and/or tuff shores. Abrasion is caused by washing of sand and gravel back and forth across the bench by waves. The result is a rather smooth sloping surface extending from below the low tide line often to several feet above it (Fig. 2C). A dense but low algal mat, usually of a varied flora, is typically present. Abrasion ramp benches are limited in size and constitute only a minor portion of shorelines. Three such benches were visited, Station 10A, on the southern shore of Rabbit (Manana) Island; Station 16, near Kawaihoa Point, on the eastern end of Maunalua Bay, Oahu; and Station A2, west of Kihei on Maalaea Bay, Maui (Fig. 3).

THE SUBTIDAL CORAL REEF PLATFORM HABITAT

More than half of the shoreline of Oahu and comparable portions of some of the other Hawaiian Islands are fringed by rather narrow coral reefs. These reefs are characterized by a predominantly sandy substratum. Living coral, patches of bare limestone and coral rubble also comprise varying proportions of the substratum, but the most actively growing corals and coralline algae are typically found at the outer edges and on the reef slopes. The reef platforms are typically subtidal and variable in depth, being usually 2-10 ft below mean sea level. Occasionally portions of the reef platform are exposed at low spring tides. The platform of some reefs is raised at the outer edge, but this rampart is often not well developed. A general discussion of Hawaiian coral reefs is given by McCaughey (1918). A typical reef fringes the south shore of Oahu, interrupted only by dredged channels and the drainage of streams. Investigation was concentrated on sections of this reef near the laboratory, noted as Stations 3 and 9 (Fig. 6). Additional collections were made at Station 4.

Brief descriptions of Stations 9 and 3, based on field notes, follow. They emphasize, respectively, the characteristics of the reef normal to the shore and parallel to the shore. The ecological notes on *Conus* which are included will serve as an introduction to the quantitative data presented below.

Diamond Head, Oahu (Sta. 9). The fringing reef on the Honolulu side of Diamond Head may be roughly divided into four zones. Zone (1) is an intertidal area of moderate surf which breaks over a substratum of detrital limestone. Landward of this zone, above the high tide limit, is a narrow sand beach. A dense growth of many species of algae occurs in zone (1), except in the bare limestone surge channels and tidal pools. This region takes the form of an abrasion ramp bench, 30-50 ft wide, which

slopes to seaward. No *Conus* were observed here, but this is perhaps due to the convenience of the area to shell collectors.

Zone (2) comprises the broad submerged reef platform, 2-6 ft below 0 tide datum. The substratum is characterized by areas of coral rubble, coral heads and sand, more or less intermingled. This region comprises most of the width of the reef, which reaches a maximum of about 1,500 ft. The areas with substratum of coral rubble are extensive. Conspicuous benthic algae are absent. These areas are also barren of large gastropods, probably because of lack of shelter provided by the pieces of rubble, which are readily moved back and forth by wave action. Scattered coral heads, usually bearing only a small colony of living coral, harbor a variety of invertebrates, including *Conus pennaceus* on the sand beneath. *C. rattus* and *C. imperialis* are occasionally epifaunal on dead coral. Sandy areas interspersed with reef limestone outcrops form the typical habitat of *Conus flavidus* and *C. lividus*, which are usually epifaunal. *C. abbreviatus* is also found, usually burrowing in sand in these areas.

Zone (3), which is variable in width, is characterized by large areas of dead coral reef, which appear to be eroding. The surface areas of these regions are often near the 0 tide datum and hence are often dry at low tide. At high tide, surf over these areas is heavy. *Conus rattus* is occasionally found, and *C. ebraeus* sometimes occurs on the vertical edges of the eroding coral areas, or in small crevices of sand below. Channels 4-6 ft deep and normal to the shore separate these areas near the outer edge of the reef and broaden into extensive areas with sand substratum just inshore. *Conus pulicarius* is found typically beneath the surface of the sand. Reef fishes abound about the steep edges.

Zone (4) is the zone of heavy surf at the outer edge of the reef, where coral flourishes. Environmental conditions precluded extensive observations.

The most common alga at Station 9 was *Lyngbya majuscula*. *Sargassum, Hypnea, Codium,* and others were also common.

Waikiki, Oahu (Sta. 3). The wide fringing reef at Station 3 appeared to offer a wide variety of microhabitats. The collecting area extended about 1,000 ft north, and about 2,500 ft south, from the Waikiki Branch of the Hawaii Marine Laboratory (Fig. 6). The width of the reef is about 600-1,000 ft. Inshore areas of the southern portion, to about the Elks Club, are characterized by more or less abundant coral rocks set in sand or sand-rubble substratum. *Conus lividus* and *C. flavidus* are often common. *C. abbreviatus* sometimes occurs in the larger sandy areas between coral rocks. Much of the reef area to seaward is eroding dead coral reef, as at Station 9, and *Conus* is generally absent. At the seaward edge of the reef are sandy areas, with some limestone outcrops. The reef slope is gentle and quite sandy. Although the area appears suitable, *Conus* occurs only occasionally. This area can be visited only on

calm days, and the usually heavy surf may make this portion of the habitat unsuitable for the snails. *C. flavidus* and *C. distans* have been found however. The latter typically occurs at reef edges and generally in rougher water than the other species of *Conus*.

From the Elks Club (Fig. 6) to just north of the laboratory, the substratum is quite different. An inner reef, shoreward of a dredged channel, is limestone bench and rubble and devoid of *Conus*. The outer reef is generally deeper, being 3-8 ft below MLLW. Sand is the dominant substratum, but coral heads are abundant and there are some rubble areas. *C. lividus, C. flavidus,* and *C. ebraeus* occur but are rather sparse. *C. distans* is sometimes found at the outer edge.

The northern portion of the area sampled supported a richer fauna. The substratum was of coral heads and rocks, reef limestone, and rubble areas. A detailed discussion of this region was given by Edmondson (1928). *Conus pennaceus* occurred under rocks in sand. Epifaunal species included *C. rattus, C. flavidus, C. lividus, C. ebraeus,* and *C. abbreviatus,* none of which was uncommon. This area especially provided sites for attachment of *Conus* egg capsules. Subsequent to the investigation, however, much of this area was dredged, and the inshore portion covered by a sand beach, to create an area for swimming.

Other reefs studied were essentially similar to the two described. Helfrich & Kohn (1955) and Kohn & Helfrich (1957) discussed the characteristics of Station K3. Extensive collecting was also carried out at reefs on Oahu at Maile (Sta. 7) and Ala Moana (Sta. 4). The location of the more important reef stations is shown in Fig. 4.

LIFE HISTORY OF *CONUS*

An account of spawning and larval development of *Conus* in Hawaii is in preparation and will be published elsewhere. Therefore, only information of ecological importance will be presented here.

SPAWNING SITE AND SEASON

Egg capsules of at least 12 species of *Conus* have been collected in Hawaii, chiefly by Ostergaard (1950) and by the writer and colleagues.

Coral reef platforms, but not marine benches, provide suitable attachment sites for egg capsules of *Conus*. Of 36 egg masses collected in the field, 29 were recorded from reef platforms. An almost complete absence of records from marine bench habitats suggests that spawning is unsuccessful there. This is probably due to the absence of protected pools in which egg capsules may be deposited without being subject to desiccation at low tide and/or torn away by heavy surf at high tide. Recruitment of bench populations is probably from pelagic veliger larvae which have been carried from other areas and are washed onto marine benches in condition to settle and assume the benthic mode of life.

All of the capsules were found between the months of February and August, although search for them was not confined to, or emphasized during, this

period. The data suggest that most species of *Conus* spawn during about the same part of the year. The spawning season of most species for which more than one egg mass has been collected is rather extended over the period between the months cited. The most complete data are for *C. pennaceus*, of which 12 egg masses were collected, all in the months of May, June, July and August. The data are probably sufficient to establish the breeding season as continuing through these months.

REPRODUCTION AND LARVAL DEVELOPMENT

As is typical in the Prosobranchia, the sexes are separate in *Conus*. The male possesses an extensible penis. Copulation was not observed. In spawning, eggs are released from the genital aperture and pass ventrally over the foot in a temporary groove to the prominent aperture of the nidamental gland on the sole. There the capsular material is extruded, enclosing a number of eggs. The capsule is attached to a hard substratum, typically under a coral rock, or to the underside of the rock itself. Illustrations of the egg capsules of *Conus* are given by Ostergaard (1950). A number of capsules (3-78, in 12 species studied) are deposited to form a cluster. The number of eggs per capsule varied from 40 to 11,400 in 5 species studied.

In 4 species studied (*C. vitulinus, C. abbreviatus, C. imperialis, C. quercinus*), the trochophore stage is entered at 2-6 days, and the veliger stage at 6-10 days, after spawning. Larvae hatch as veligers about two weeks after spawning. These observations are in agreement with those of Ostergaard (1950), who also reported development of 4 other species, which hatched 12-16 days after spawning. Almost all of the eggs in a capsule develop completely, and no nurse eggs were observed.

With the exception of one species, the length of the pelagic stage could not be determined. The maximum survival time of free-swimming veligers in the writer's laboratory was 9 days. Metamorphosis was observed only in *Conus pennaceus*, which has an extremely short free-swimming stage of less than one day. On the second day after hatching, metamorphosis is virtually completed and the young snail begins to craw about on its foot. These juveniles survived for periods of up to 20 days, but no significant growth was observed after hatching. The nature of the food at this stage is unknown. Protozoa abounded in the cultures. Thorson (1946) concluded that all prosobranch larvae known from the Oresund feed on phytoplankton, and he calculated the theoretical maximum diameter of the food to be 5-45μ. The mouths of *Conus* veligers measured were of about the same diameter as the esophagus of the smaller larvae measured by Thorson. Thus the larvae of *Conus* probably depend for food on phytoplankton, nannoplankton and detritus. Examination of squash preparations of *C. pennaceus* a few days after settling revealed the presence of radula teeth. These differ in form from the adult teeth, being shorter in pro-

portion to the thickness, and they are probably not functional. Thus neither the method of feeding nor the food is known at this stage of the life history.

POST-LARVAL DEVELOPMENT AND GROWTH

It was possible to study post-larval development only in *Conus pennaceus*. At hatching, the larvae of this species are several times as large as those of other species, measuring about 1.3 mm in shell length.

A rough estimate of the rate of post-larval growth was obtained in the following manner. Four clusters of egg capsules of *Conus pennaceus* were collected in a large tide pool adjacent to Station 9 on 13 August 1955, and additional clusters were observed but not removed. Adults collected at the same time ranged from 33 to 37 mm in shell length. On 30 November, 3.5 months later, 8 specimens of *C. pennaceus* were collected in the same tide pool. Of these, 6 were probably hatched from egg capsules the previous summer (Fig. 7). On 27 December, 41 specimens of *C. pennaceus* were collected in this tide pool.
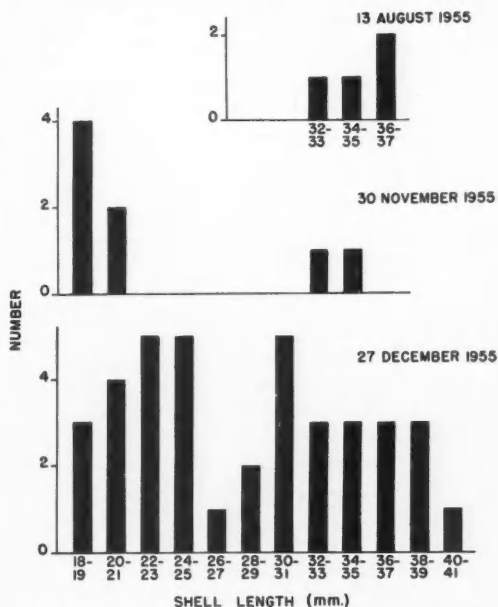
FIG. 7. Length-frequency distribution of *Conus pennaceus* at Station 9, 13 August-27 December 1955.

The length-frequency distribution of the December population is also shown in Fig. 7. Although bimodality suggesting two age classes is evident, it is quite possible that all of the specimens were spawned the previous summer. The minimum at 26-27 mm may not indicate separation of two age classes, because of the large number of specimens of greater length collected. If these were older specimens, most of them probably would have been collected from the tide pool on previous occasions. As noted above, the breeding season is long. The mean shell length of

first age-class individuals in November was 19 mm, with S.D. = 6.3 mm. In December, mean shell length was 28 mm, with S.D. = 7.7 mm. The mean mean growth rate was thus 5-6 mm/month during the first 3.5 months. During the next month the mean increment was 5 mm.

It was not possible to obtain any other growth data of this type, since such isolated populations are exceptional. Shells of a number of specimens of *Conus ebraeus, C. abbreviatus,* and *C. sponsalis* from a marine bench (Sta. 5) were marked with a diamond point vibrator and returned to their natural habitat. Of these, three specimens, all *C. ebraeus,* were recovered after 133-221 days following release. The growth increments ranged from 0.3-0.6 mm shell length and 0.2-0.4 g wet weight per month. Although only these data are available, they presumably give the correct order of magnitude of growth of older individuals.

If the growth rates cited hold for other species, it may be concluded that, in species comparable in size to *Conus pennaceus* and *G. ebraeus* (Fig. 9), several millimeters per month in shell length are added during the first few months, the rate later falling off to a few tenths of a millimeter per month.

ABUNDANCE AND POPULATION DENSITY OF *CONUS*

Darwin (1859: 319) pointed out that most species of animals are characterized by being rather rare. Since species of *Conus* are not exceptions, and because time available for collecting was limited, several of the less abundant species are represented by rather small samples. In order to determine the ecological relationships of the species, the data presented in this report have therefore been subjected to appropriate statistical analyses.

As MacArthur (1957) has shown, the expected abundance of the rth rarest species in the community of a single habitat which has been adequately sampled, and in which ecological niches are nonoverlapping and continuous, is

$$\left(\frac{m}{n}\right) \sum_{i=1}^{r} \left(\frac{1}{n-i+1}\right) \qquad (1)$$

where m = the total number of individuals, n = the number of species, and i = the species rank. All of the data on abundance of *Conus* have been presented in comparison with the distribution expected according to this theory.

THE MARINE BENCH HABITAT

Solution Benches. The population of *Conus* at Station 5 was the densest stable population studied on Oahu. Eight species were collected, of which *C. ebraeus* was the most abundant. In 61 quantitatively sampled 100-sq ft quadrats, four species were collected. The relative abundance of species is shown in Fig. 8. If only data from the quantitatively sampled areas are included (Fig. 8A) a homogeneous population or single community is indicated by agreement

FIG. 8. Abundance of species of *Conus* at Station 5. A. Data from quantitatively sampled quadrats. m = 136, n = 4. Species rank: 1 = *ebraeus,* 2 = *abbreviatus,* 3 = *sponsalis,* 4 = *chaldaeus.* B. Curves (A) and (B), data from all collections at Station 5. m = 500, n = 8. Curves (C) and (D), data from all collections, but with exclusion of three species characteristic of other habitats. Explanation in text. m = 484, n = 5. Species rank: (A) and (B) 1 = *ebraeus,* 2 = *abbreviatus,* 3 = *sponsalis,* 4 = *chaldaeus,* 5 = *lividus,* 6 = *flavidus,* 7 = *rattus,* 8 = *pennaceus;* (C) and (D) 1 = *ebraeus,* 2 = *abbreviatus,* 3 = *sponsalis,* 4 = *chaldaeus,* 5 = *rattus.*

of the observed curve with the expected distribution for the community of a uniform habitat.

Curve (A) in Fig. 8B is based on summation of results of all 18 collecting trips made to Station 5. The slope is steep, since common species are too common and rare species too rare. The curve is therefore not in good agreement with the theoretical distribution (Curve B), and a heterogeneous population, or the inclusion of occupants of more than one habitat, is indicated. The heterogeneous aspect of the total population may be explained as follows: Three of the species included occur more typically in habitats other than the solution bench platform. All three, *Conus pennaceus, C. flavidus,* and *C. lividus,* are typically subtidal species, which are rarely exposed by receding tide, and they occur much more commonly where such a habitat is provided, as will be shown below. If the abundance curve is plotted without these species, the resulting line (C) is considerably straighter and approaches the theoretical curve (D) more closely. It is therefore apparent

that the sparse occurrence of three species which are more typical residents of a different habitat contributes to the heterogeneity shown by the curve (A) for total abundance at Station 5.

The mean density of *Conus* on this bench is 2.2 individuals/100 sq ft, based on the 61 quantitatively sampled quadrats. The mean population density of species censused in quadrats is shown in Table 1A.

TABLE 1. Population Density of Species of *Conus* at Two Marine Bench Stations.

Species	Mean number per 100 sq. ft. ($=9.3 m.^2$)
A. Station 5	
Conus ebraeus	1.02
Conus abbreviatus	0.66
Conus sponsalis	0.41
Conus chaldaeus	0.15
	2.24
B. Station K1	
Conus abbreviatus	0.85
Conus ebraeus	0.55
Conus sponsalis	0.48
Conus catus	0.24
Conus chaldaeus	0.18
Conus rattus	0.09
Conus flavidus	0.03
Conus retifer	0.03
	2.44

The mean biomass of all species was calculated to be about 0.6 g dry organic matter/100 sq ft, or 0.065 g/m².

The species differ in size. Length-frequency distributions are shown in Fig. 9. The population is essentially an adult one, and juvenile specimens are rarely found. Despite numerous collecting trips at all times of year, no egg capsules of *Conus* were ever found.

At Station 11, nine species of *Conus* were collected, of which *C. sponsalis* was the most abundant. In eight 100-sq ft quadrats, quantitatively sampled in September, four species were present, with mean density of 5.5 individuals/100 sq ft and abundances as shown in Fig. 10. The curve shows that the observed number of *C. sponsalis* (38) is much higher than that expected in a homogeneous population containing the observed numbers of the other species.

An even denser population was observed on 29 November 1955. At this time, counts of two areas, each of but one sq ft, were 3 and 7 individuals of *Conus sponsalis*. No other species were present. This abundance (= 500/100 sq ft) was present only on the extremely wide area of bench described above.

This high density of *Conus sponsalis* is believed to be related to the fact that the individuals were much smaller (mean length 13.5 mm) than elsewhere (mean length 22.1 mm at Sta. 5). Length-frequency distributions of specimens collected at Station 11 in September and November are shown in Fig. 11A. The September population is unimodal. However, the
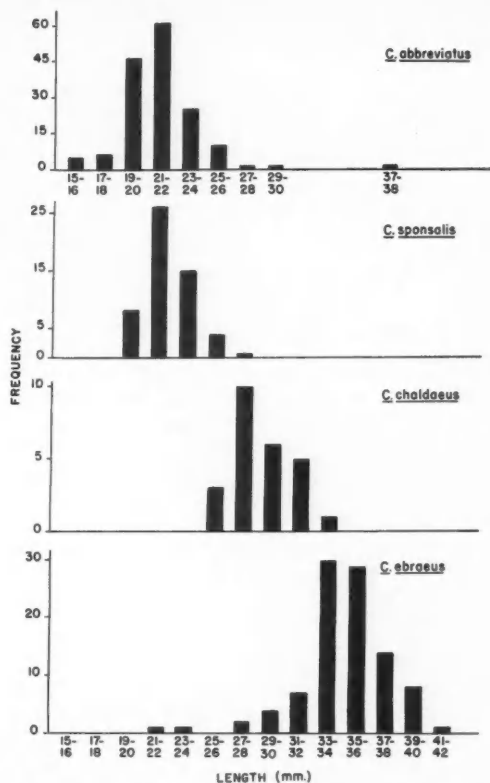
FIG. 9. Length-frequency histograms of the dominant species of *Conus* at Station 5.

November population is bimodal, with an absence of individuals of 12-13 mm. This suggests that a new age class of 6-11 mm individuals has been added to the population. Unfortunately, no information is available on the reproductive cycle of *C. sponsalis*. However, egg capsules of many species of *Conus* are found in summer and if eggs were laid in August, hatching might take place in September, with settling of pelagic veliger larvae in October giving rise to a dense population of juvenile individuals in November. Although no egg capsules were found at Station 11, the bench is interrupted by rather deep, somewhat protected pools, which may provide suitable spawning sites. Alternatively, larvae may arrive in numbers from other areas in settling condition.

Population density varied greatly in the area of Station 11. Particularly densely populated sections were quantitatively sampled by the transect method. In these regions, two transects of eight quadrats gave the mean density of 5.5 individuals (of four species)/100 sq ft. The maximum observed density of about 500 juveniles/100 sq ft has been mentioned.

On other occasions, searches of 0.63 and 1.25 man-hrs resulted in only one and three specimens, respectively. Since the time required to sample a 100-sq ft quadrat was usually 5 minutes (0.08 hr), this
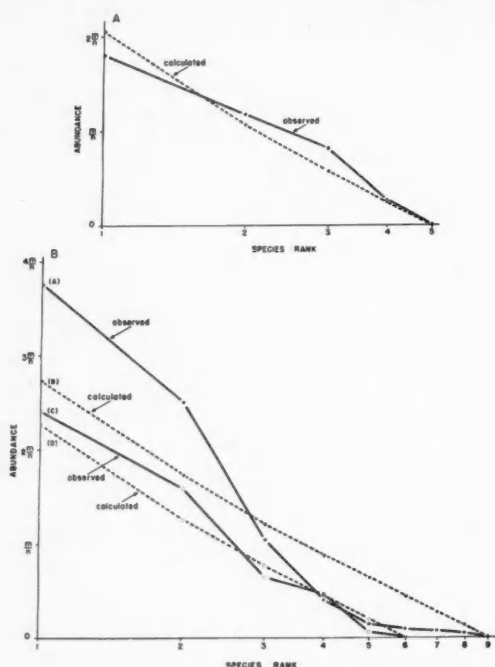
Fig. 10. Abundance of species of *Conus* at Station 11. Data from quantitatively sampled quadrats. m = 44, n = 4. Species rank: 1 = *sponsalis*, 2 = *chaldaeus*, 3 = *ebraeus*, 4 = *rattus*.

Fig 11. Length-frequency histograms of *Conus sponsalis*. A, Station 11. B, Station A3.

factor can be used to convert time-relative to space-relative density. A search of 0.63 man-hr would thus cover 7,900 sq ft and 1.25 man-hrs 15,600 sq ft. Corresponding densities are 0.01 and 0.02 individuals/100 sq ft, respectively.

Water-leveled Benches. Six species of *Conus* were collected at Station A3, of which *C. sponsalis* was by far the most abundant. The abundance of species is plotted in Fig. 12. Fig. 12A represents total abundance, and 12B the abundance in a single quantitatively sampled 100-sq ft quadrat on the water-leveled part of the bench (Fig. 4). Both curves show an obvious inflection point, which is caused by the relatively great abundance of *C. sponsalis*. Disagreement with the calculated theoretical distribution suggests a heterogeneous population.

Density on the water-leveled bench at Station A3 was second only to that in the two 1-sq ft quadrats sampled at Station 11. At Station A3, only the single quadrat was sampled. However, this represented a considerable fraction of the total available area (Fig. 4). One specimen of *Conus flavidus* and 25 *C. sponsalis* were present in this area.

The length-frequency distribution of *Conus sponsalis* at Station A3 is unimodal (Fig. 11B). The population is probably an adult one, although the individuals are not as large as those at Station 5. The relative superabundance of *C. sponsalis* cannot therefore be ascribed to an influx of first age class juveniles. Since the observations were made on 5 August, during the probable spawning season, this is even less likely.

Marine benches do not in general provide suitable

sites for deposition of egg capsules of *Conus*. However, a specimen of *C. catus* was collected at Station A3 in spawning condition, as evidenced by the deposition of an egg capsule which was attached to the shell after collection.

Station K1. At Station K1, all *Conus* present in 33 quadrats, each of 100 sq ft, were counted. Eight species were present in the area sampled, of which the most abundant was *C. abbreviatus*. Relative abundance of species is shown in Fig. 13. The distribution calculated from Equation (1) is also included, and the data are seen to be in excellent agreement with it. This supports the observation that the habitat is a rather uniform one, with a homogeneous population, or single community, of *Conus*.

The solution bench at Station 5 was the only area
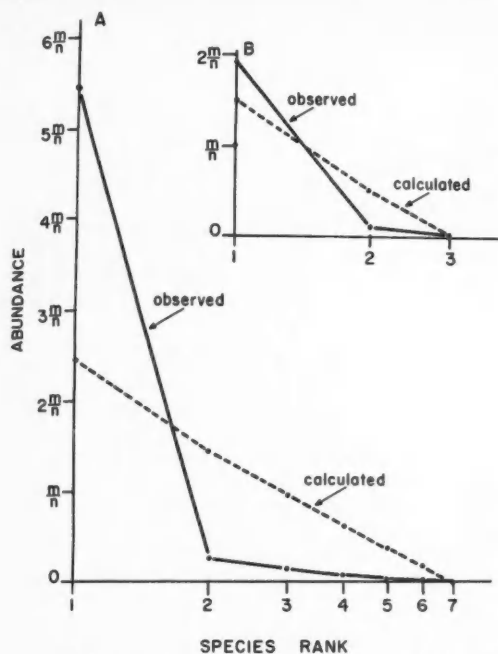
FIG. 12. Abundance of species of *Conus* at Station A3. A, Total data. $m = 166$, $n = 6$. B, Data from quantitatively sampled quadrat. $m = 26$, $n = 2$. Species rank: A. $1 = sponsalis$, $2 = rattus$, $3 = catus$, $4 = flavidus$, $5 = abbreviatus$, $6 = chaldaeus$; B. $1 = sponsalis$, $2 = flavidus$.
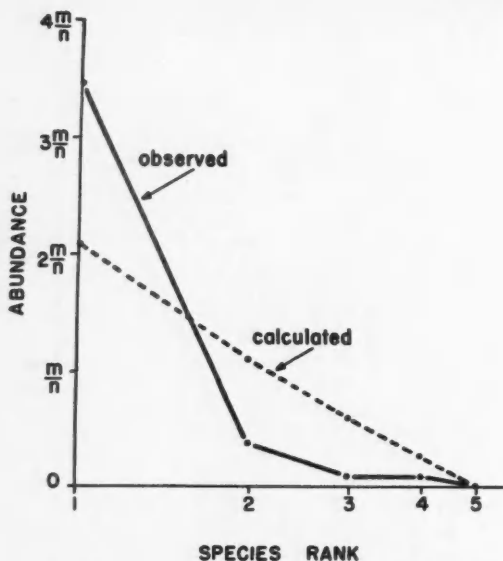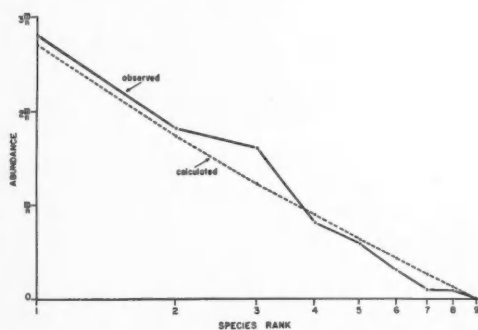

FIG. 13. Abundance of species of *Conus* at Station Kl. Data from quantitatively sampled quadrats. $m = 81$, $n = 8$. Species rank: $1 = abbreviatus$, $2 = ebraeus$, $3 = sponsalis$, $4 = catus$, $5 = chaldaeus$, $6 = rattus$, $7 = flavidus$, $8 = retifer$.

sampled more intensively than Station K1. The three most abundant species are the same at the two sites, although the order is different. The mean density of all *Conus* species at Sta. K1 is 2.44 individuals/100 sq ft, based on the 33 quantitatively sampled quadrats. The mean density of each species is shown in Table 1B. The mean density of *C. abbreviatus* is higher, while that of *C. ebraeus* is lower, than at Sta-

tion 5. The densities of *C. sponsalis* and *C. chaldaeus* are about the same at the two stations.

Abrasion Ramp Benches. The rather smooth sloping surface and attendant wave action of abrasion ramp benches provide a rather unfavorable habitat for large gastropods. However, some shallow crevices provide shelter at high tide. A total of but 47 specimens of seven species of *Conus* were collected in five field trips to abrasion ramp benches. On all such benches studied, *C. rattus* was the most abundant species. *C. sponsalis* and *C. abbreviatus* were relatively common, and *C. chaldaeus*, *C. flavidus*, and *C. lividus* were also present.

SUMMARY

Data on abundance and population density of *Conus* on all marine benches studied are summarized in Table 4. Between six and nine species are found in such habitats. However, the figures in the fourth column of Table 2 probably indicate the number of species comprising a homogeneous population, at least at the more thoroughly studied stations. On very narrow water-leveled and solution benches, *C. sponsalis* is the dominant species, and only 1-3 other species may be present. Wider benches are occupied by proportionally greater numbers of species. As will be shown below, the species are then distributed non-randomly across the bench platform from shore to seaward edge.

TABLE 2. Summary of Abundance and Population Density of *Conus* on Marine Benches

Station	Width of Bench (ft.)	Total Number of Species	Number of Species in Quadrats	Number of Quadrats Sampled	Density (No./100 sq. ft.)	Most Abundant Species
Solution Bench Stations						
5	60	8	4	61	2.24	*ebraeus*
11	40	9	4	8	5.5 (0.01*-500)	*sponsalis*
Water-leveled Bench Stations						
K1	200	9	8	33	2.44	*abbreviatus*
A3	15	6	2	1	26	*sponsalis*
Abrasion Ramp Bench Stations						
Total	...	6	..	0	1.0*	*rattus*

*Calculated from time-relative density.

The species of greatest abundance is variable among benches of similar, as well as different, geological origin. Abrasion ramp benches were not studied in detail, hence data from them are combined in Table 2. However, *Conus rattus* was the most abundant species at all three such benches visited, and it may be termed typical of this formation. This species was of minor importance on both solution benches and water-leveled benches.

Sampling of a large number of 100-sq ft quadrats at Stations 5 and Kl indicated that a fairly stable population of 2-2.5 individuals/100 sq ft may be ex-

pected on solution benches and water-leveled benches. Other areas sampled quantitatively were those in which extremely large populations were observed by inspection. Conversion of time-relative to space relative density suggests a lower limit of population density on marine benches of about 0.01 individual/ 100 sq ft.

THE SUB-TIDAL REEF PLATFORM HABITAT

Inspection of a number of coral reef platforms led to the conclusion that the abundance and distribution of *Conus* in these habitats are characterized by patchiness. This not unexpected phenomenon must be considered in interpreting the data presented in this section and in the following one on distribution.

In Figs. 14-17, data on abundance at the four thoroughly sampled reef stations are presented. No one species is most abundant on all of the reefs. At each station, however, either *Conus flavidus* or *C. lividus*, or both, represent one or both of the two most abundant species. This is in marked contrast to marine bench stations where, as has been shown above, these two species occur infrequently.

FIG. 14. Abundance of species of *Conus* at Station 3. m = 182, n = 9. Species rank: 1 = *flavidus*, 2 = *lividus*, 3 = *ebraeus*, 4 = *abbreviatus*, 5 = *rattus*, 6 = *imperialis*, 7 = *striatus*.

At only one of the adequately studied reef stations is the most abundant species neither *Conus lividus* nor *C. flavidus*. At Station 7, the most abundant species was *C. sponsalis*. This is attributed to substratum factors, which will be discussed in detail below.

At all stations, agreement of the results of analysis of abundance data with the curve calculated from Equation (1) is sufficient to justify the conclusion that the subtidal reef platform constitutes a single rather than composite habitat, which supports a homogeneous community or interspecific population of *Conus*. The striking agreement of the observed and calculated curves for Station 7, which is the closest of any census thus far analyzed in this manner (MacArthur, personal communication), is probably fortuitous.

Population Density. Population density of *Conus* was more difficult to study directly on subtidal reef
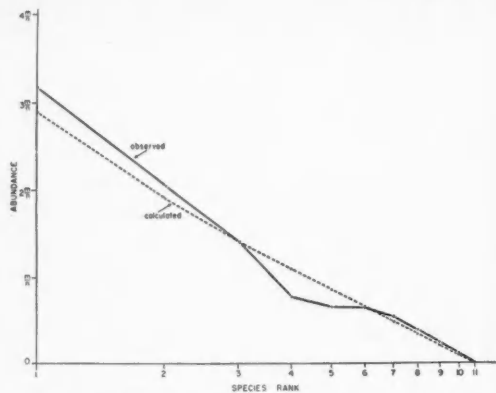
FIG. 15. Abundance of species of *Conus* at Station 4. m = 78, n = 10. Species rank: 1 = *lividus*, 2 = *flavidus*, 3 = *abbreviatus*, 4 = *imperialis*, 5 = *ebraeus*, 6 = *rattus*, 7 = *vitulinus*, 8 = *sponsalis*, 9 = *chaldaeus*, 10 = *vexillum*.
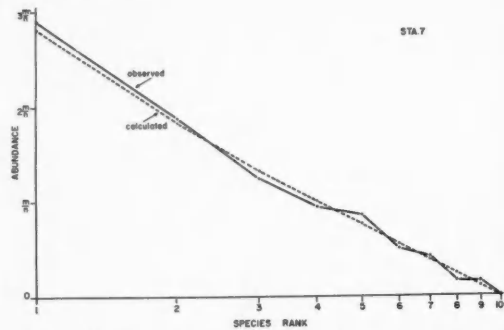
FIG. 16. Abundance of species of *Conus* at Station 7. m = 182, n = 9. Species rank: 1 = *sponsalis*, 2 = *lividus*, 3 = *ebraeus*, 4 = *flavidus*, 5 = *pennaceus*, 6 = *abbreviatus*, 7 = *rattus*, 8 = *distans*, 9 = *chaldaeus*.

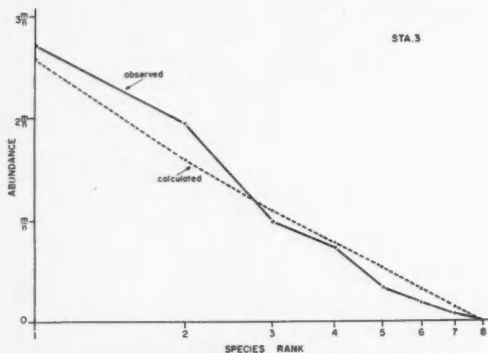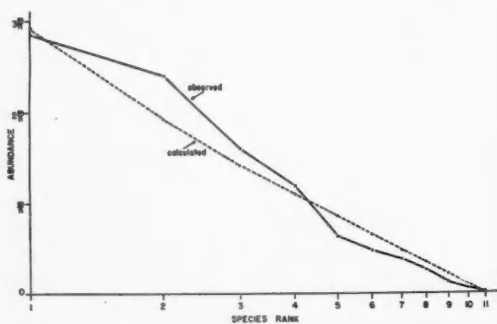Fig. 17. Abundance of species of *Conus* at Station 9. m = 187, n = 10. Species rank: 1 = *flavidus*, 2 = *pennaceus*, 3 = *lividus*, 4 = *abbreviatus*, 5 = *pulicarius*, 6 = *ebraeus*, 7 = *imperialis*, 8 = *vexillum*, 9 = *rattus*, 10 = *marmoreus*.

platforms than on marine benches. This was due both to technical difficulties and to the obvious patchiness of the populations. During most field trips,
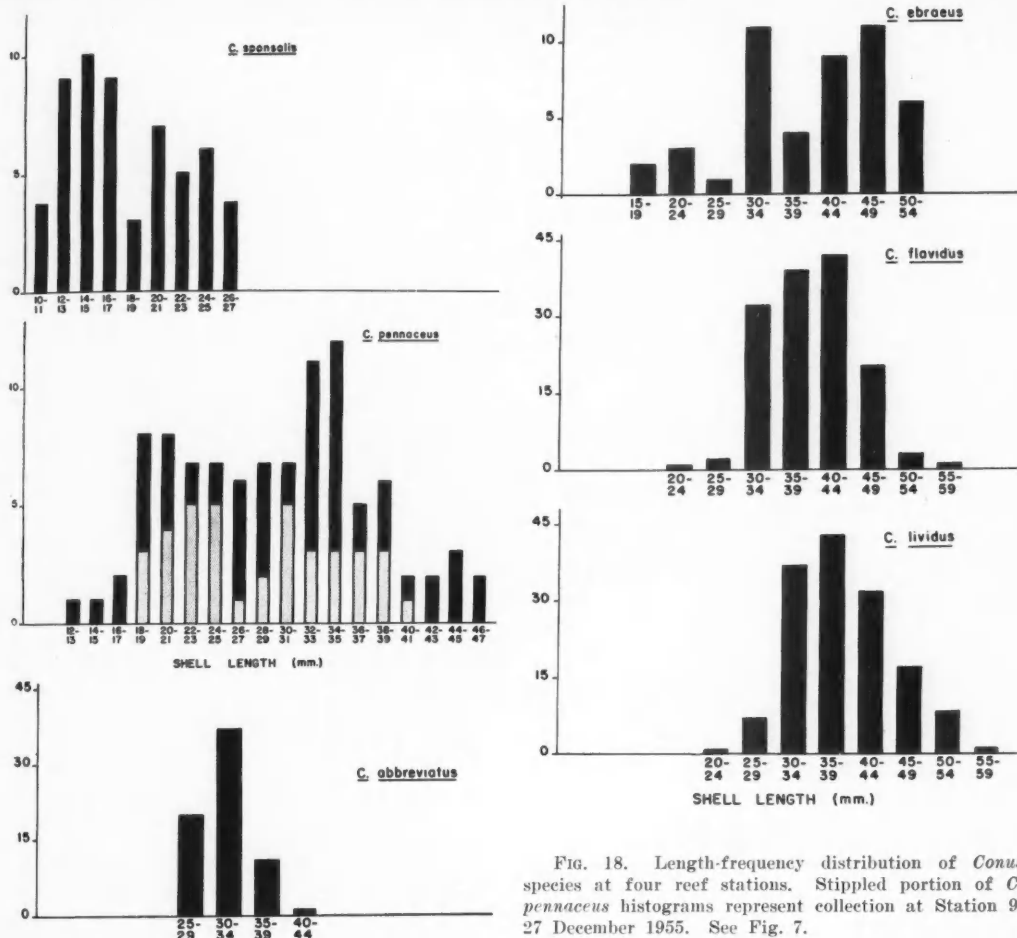
FIG. 18. Length-frequency distribution of *Conus* species at four reef stations. Stippled portion of *C. pennaceus* histograms represent collection at Station 9, 27 December 1955. See Fig. 7.

collecting efforts were of necessity concentrated in areas of greatest abundance. Conversion of time-relative to space-relative density would thus give values considerably in excess of the mean density on the entire reef platform.

At one reef station (Sta. K3, see Helfrich & Kohn 1955) transects of known area were sampled quantitatively. The results (Table 3) show that the mean population density of all species in the area sampled was 0.16 individual/100 sq ft. This is lower by an order of magnitude than the density on marine benches. This relationship is probably generally valid, although favorable parts of reef platforms may support local populations which approach those of marine benches in density.

The mean biomass of *Conus* in the quantitatively sampled areas at Station K3 was calculated to be 0.06 g dry weight organic matter/100 sq ft (0.0065 g/m²). Although the population density on marine benches is about 15 times as large as on reef platforms, the biomass of *Conus* is only ten times as

TABLE 3. Population Density of *Conus* at Station K3.

Area Sampled (sq. ft.)	Species	Density (No./100 sq. ft. =9.3 m.²)
3,000	*C. ebraeus*	0.07
	C. abbreviatus	0.07
	C. chaldaeus	0.03
	C. flavidus	0.03
		0.20
3,000	*C. ebraeus*	0.10
1,200	*C. (species not noted)*	0.17

Mean Density of All Species=0.16

great. Although the comparisons are extremely rough, the discrepancy is probably real. Comparison of Figs. 9 and 18 clearly shows the prevalence of larger individuals in the populations occupying reef habitats. The mean shell length of two species common in both habitats is compared in Table 4. These values are 13% and 54% larger in reef platform than in marine

bench populations of *C. ebraeus* and *C. abbreviatus*, respectively. This may reflect the more equable environmental characteristics of the former habitat. The mean shell length of *C. sponsalis* on reefs was 17.8 mm. In bench populations, mean shell length ranged from 13 to 22 mm. The explanation may be that *C. sponsalis* occupies those parts of reef platforms where conditions most closely approximate those of marine benches.

TABLE 4. Mean Shell Length of Reef and Bench Populations of *Conus ebraeus* and *C. abbreviatus*.

	LENGTH IN MILLIMETERS			
	All Reefs		Sta. 5 (bench)	
	Mean	S.D.	Mean	S.D.
C. ebraeus...	39.0	9.7	34.6	3.2
C. abbreviatus	32.7	3.1	21.3	3.5

Except for the growth studies reported above, collection data were not analyzed for seasonal variations, since observations were made only during a single complete annual cycle.

COMMUNITY DIVERSITY AND HETEROGENEITY

The similarity of the species composition of different populations may be conveniently measured by an index of diversity given by Koch (1957):

$$I = \frac{t-n}{n(P-1)} \qquad (2)$$

where n = the total number of species represented, P = the number of populations or communities sampled, and t = the arithmetic sum of n_1, n_2, n_3, ... n_p, which are the numbers of species in each population or community. If I is low, the species composition differs greatly from population to population. I approaches unity with increasing similarity of the populations compared.

This index was calculated separately for the four most thoroughly sampled reef stations (Sta. 3, 4, 7, and 9) and the four most thoroughly sampled bench stations (Sta. 5, 11, K1, and A3). In both cases, I was 0.58. Comparison of total collections from all bench stations with those from all reef stations gave I = 0.61. The three indices are so similar that there would appear to be no greater ecological difference between the reef and bench habitats than among different reefs, or among different benches. This is misleading, however, since the index used measures only similarity of qualitative species composition.

Consideration of quantitative data concerning the relative abundance of species in different habitats suggests a different interpretation. It has been shown that individual reefs and benches generally support homogeneous populations of *Conus* (Figs. 8, 10, 12-17). Inspection of these graphs shows that three species, *C. sponsalis*, *C. ebraeus*, and *C. abbreviatus*, are rather consistently the most abundant species on

marine benches, while two entirely different species, *C. lividus* and *C. flavidus*, are dominant at almost every reef station.

A comparison of the relative abundance of all species at all reef and bench stations is shown in Fig. 19. Of the 18 species considered, 6 are proportionally more abundant on marine benches than on reef platforms. In 4, the discrepancy in abundance between the two types of habitats is at least one order of magnitude. Twelve species are relatively more abundant on reefs than on benches. The discrepancy is at least one order of magnitude in 8 of these.
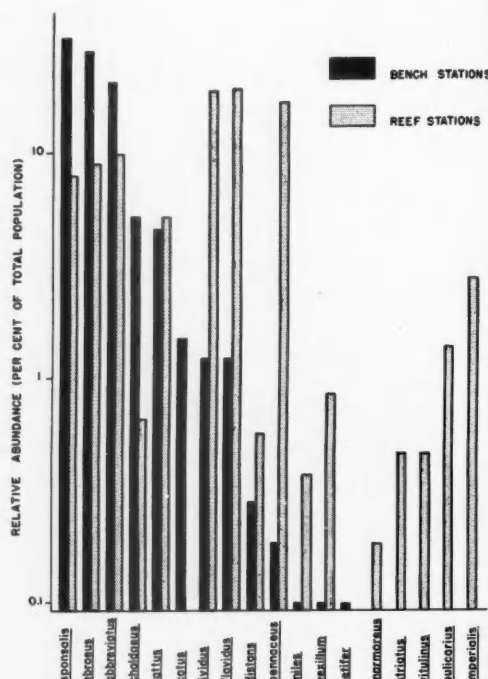
FIG. 19. Relative abundance of *Conus* species at all bench stations (solid histograms) and all reef stations (stippled histograms).

A more quantitative measure of community heterogeneity, H', based on information theory, is given in Equation (3), which is modified from Margalef (1956):

$$H' = I_{m(AB)} - \left(\frac{I_{m(A)} + I_{m(B)}}{2}\right) \qquad (3)$$

in which

$$I_m = \frac{1}{m}\log\frac{m!}{m_1!\cdot m_2!\cdot\ldots\cdot m_s!} \qquad (4)$$

where m = the number of individuals of all species, m_1 = the number of individuals of the most abundant species, and m_s the number of the rarest species. The subscripts are equivalent to the values on the abscissas of Figs. 8, 10, and 12-17 and the values can be determined from data given in the graphs.

In Equation (3), A and B signify different communities. Equation (3) can be expanded for application to more than two communities. Equation (5) gives H' for four communities, A, B, C, and D:

$$H' = I_{m(ABCD)} - \left(\frac{I_{m(A)} + I_{m(B)} + I_{m(C)} + I_{m(D)}}{4} \right) \quad (5)$$

sampled bench stations (Figs. 8, 10, 12, 13), H' = 0.19.

Application of Equation (3) to summations of abundances at the four most thoroughly sampled reef stations (combined as community "A") and the four most thoroughly sampled bench stations (combined as community "B") gave H' = 0.84.

The low heterogeneity of the *Conus* communities at individual stations has been demonstrated above. In addition, a low value resulted when the measure of heterogeneity introduced by Margalef (1956) was calculated for summed abundance data from four reef stations. Calculation from summed data from four benches gave a similar low value. However, comparison of summed data from four reefs with summed data from four benches resulted in a high value, indicating marked heterogeneity between the communities of *Conus* in these two kinds of habitats.

To summarize, two types of habitats, reef platforms and marine benches, were distinguished on the basis of observational data presented in the previous section. The data reported in the present section are interpreted as justifying this separation by indicating its significance to the gastropods under consideration, as well as to the investigator.

LOCAL DISTRIBUTION OF *CONUS*

MARINE BENCHES

Distribution of *Conus* across bench platforms was studied by the transect method. Two parallel lines, marked at 10-ft intervals and 10 ft apart, were secured across the bench from inshore edge to near the seaward margin. Ten-foot square areas of the platform were thus delimited. In each transect series, all of the *Conus* visible in each 100-sq ft area were counted. Counts were made at night, when the gastropods were actively crawling about on the bench. For convenience, it was assumed that all of the snails in the study areas were visible from above and none were buried in the algal turf or under stones or coral, as is often the case in the daytime.

Solution Benches. Distribution of *Conus* species, based on data from transects made at Station 5, is shown graphically in Fig. 20. Only the four most abundant species at Station 5 were observed in the transects. The populations of these species are not randomly distributed across the bench platform from pitted zone to outer edge. Interspecific differences are apparent from Fig. 20. Although *C. abbreviatus* is the more abundant, it and *C. sponsalis* are similarly distributed (Wilcoxon test: P ≫ .05). Most of the populations of these two species occupy a strip within 20 ft of shore, independently of the width of the bench. In contrast, the peak density of *C.*

Application of Equation (5) to the abundance data presented (Figs. 14-17) for populations of *Conus* at the four most thoroughly sampled reef stations gave H' = 0.09. For the four most thoroughly
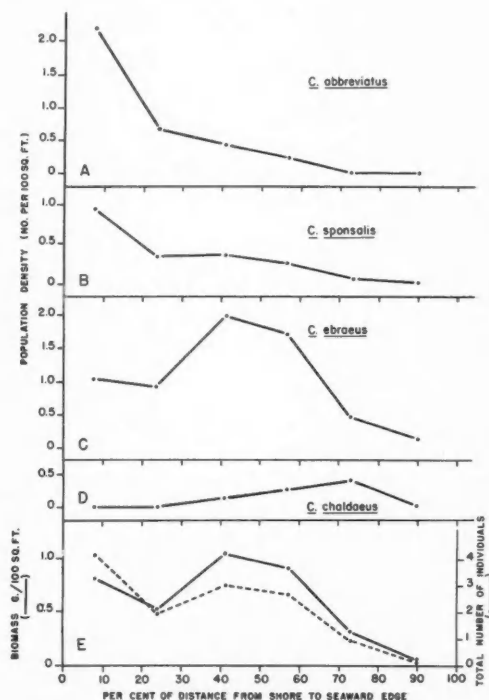
FIG. 20. Distribution of species of *Conus* across bench at Station 5. Each point to the left of 90% represents the average of 8 or 9 transects. The points at 90% represent the average of 5 transects. If width of bench varied from 60 ft at transect site, data were adjusted to a width of 60 ft.

ebraeus occurs about halfway across the bench. Lower densities occur near shore and near the outer edge. The density peak of the least abundant species, *C. chaldaeus,* is nearer the outer edge, but the edge itself is not occupied. This species rarely occurs in the shoreward zone occupied by *C. abbreviatus* and *C. sponsalis.* Wilcoxon tests showed that the distribution of *C. ebraeus* differs significantly from that of *C. sponsalis* (P < .05) and from that of *C. chaldaeus* (P < .01).

The biological significance of this pattern of distribution will be discussed below. The total density of all species of *Conus* tends to decrease toward the outer edge. Fig. 20E shows this distribution in density as well as in terms of dry weight, excluding shells.

At Station 11, the distribution of *Conus sponsalis* across the bench is shown in Fig. 21 to be essentially similar to that at Station 5. Most of the population

occupies the more protected shoreward portion of the bench. The striking difference between the populations at Stations 5 and 11 is the virtual absence of *C. ebraeus* and *C. abbreviatus* at the latter (Fig. 10), although the type of habitat afforded seems suited to these species.
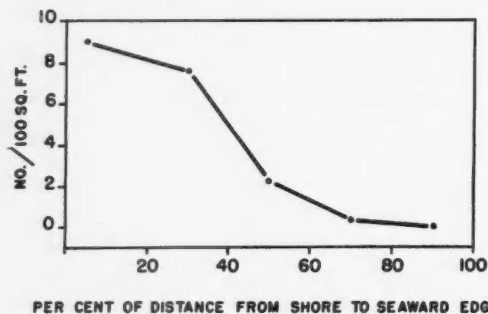
FIG. 21. Distribution of *Conus sponsalis* across bench at Station 11. Data from transects.

Water-leveled Benches. The patterns of distribution across the bench at Station K1, as determined by transecting (Fig. 22), are also quite similar to those at Station 5. As at Station 5, the distribution of *Conus sponsalis* and *C. abbreviatus* are not significantly different from each other (P $\gg$ .05). The distribution of *C. ebraeus* differs significantly from that of *C. sponsalis* (P< .01) as well as from that of *C. chaldaeus* (P< .01).

A striking difference between the distribution patterns at Stations 5 and K1 is that although the bench at Station K1 is three times as broad as Station 5, the four dominant species occur in bands which are only about twice as wide as those at Station 5. Since population density is similar, the density peaks of *C. abbreviatus* and *C. sponsalis* are therefore considerably higher at Station K1 (5.8 and 3.5, respectively) than at Station 5 (2.3 and 0.9, respectively). Thus, in contrast with Station 5, a broad area of bench platform is present which is occupied only by *C. chaldaeus* of the four dominant species under consideration.

In this region, four other species were found. The most abundant was *Conus catus*. Densities of the others, *C. rattus*, *C. flavidus*, and *C. retifer*, were very low. Thus three of the species characteristic of the solution bench habitat do not extend to the seaward portion of the broad water-leveled bench at Sta. K1 but are replaced there by four other species, only one of which is common.

The density distribution of all species is shown in Fig. 22G. The density peak is relatively nearer shore than at Station 5. Total density decreases toward the seaward edge at both stations.

Station A3. Search of the rampart zone at Sta. A3 revealed no specimens of *Conus*. In addition to *Morula tuberculata*, which is the dominant gastropod, the only other common large gastropod was *Mitra*
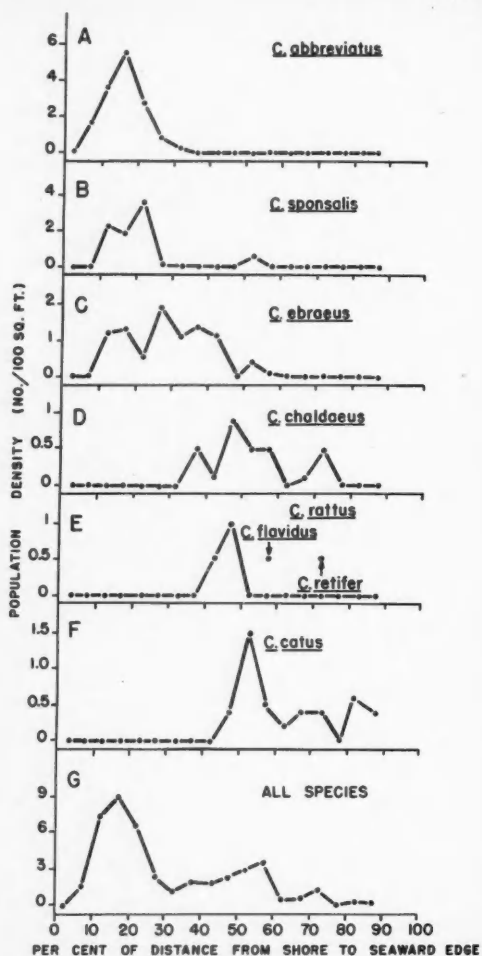
FIG. 22. Distribution of species of *Conus* across bench at Station K1. Data represent the average of two transects.

litterata. The factor which excludes *Conus* from this microhabitat is not known. Almost all of the specimens of *Conus sponsalis* were collected on the flat water-leveled platform. They were found with the shells partly buried in the algae-sand turf, and they thus apparently avoid desiccation during the day. The other species, in contrast, were found more typically on the inner margin of the rampart and level bench platform, or in other sites where the irregular tuff provides shelter during the day. These species may be too large to obtain adequate protection from the thin algal mat. The heterogeneity shown by the abundance curve (Fig. 12) can be accounted for by these microhabitat differences. It is of interest that the single specimen of *C. flavidus* collected in the quadrat was only 13 mm long, less than one-half the normal adult length of this species.

REEF PLATFORMS

The most apparent characteristic of the distribution of *Conus* on reef platforms, patchiness, has been mentioned above. It is believed to be related primarily to the nature of the substratum, discussed in more detail in the following section.

Technical difficulties and low population density on reef platforms precluded the use of the transect method for determining patterns of distribution normal to the shoreline. The less exact method of noting the approximate site of individual specimens, in terms of per cent of the distance from shore to outer edge where the specimen was collected, was employed. These data were recorded in the field by the method described by Kohn (1956a). In this manner the approximate distribution of 274 specimens of 11 species at four reef stations was determined. Most of the data concerned five species at three stations, as shown in Table 5. Data for Station 7 are tabulated separately. At the other stations, samples were somewhat biased since collecting effort was greater on the inshore half of the reef than the offshore half. At Station 7, the effort was not so biased, and the similarity with data from the other stations suggests that the latter are valid. The evidence thus indicates that more intensive collecting on the offshore parts of other reefs would reveal *Conus* in low density, and this was confirmed by inspection.

TABLE 5. Distribution of Five Species of *Conus* Across Reef Platforms at Stations 3, 7, and 9.

Per cent of Distance From Shore to Outer Edge	abbreviatus		flavidus		lividus		ebraeus		sponsalis		Total
Sta.	7	T	7	T	7	T	7	T	7	T	
0- 30.........	4	8	6	26	12	23	7	10	2	2	69
30- 60.........	0	4	6	16	10	18	2	10	20	20	68
60- 90.........	3	3	3	5	4	5	7	8	29	29	50
90-100.........	1	2	0	0	3	4	1	2	2	2	10
	8	17	15	47	29	50	17	30	53	53	197

T=Stations 3+7+9

The distribution patterns normal to the shore of *Conus abbreviatus, C. flavidus, C. lividus,* and *C. ebraeus* do not differ significantly from each other in the samples observed (P ⁓ .05). The distribution of *C. sponsalis* at Station 7 may differ significantly (P > .05) from that of *C. ebraeus* and thus from those of all other species. This variation, however, is in the opposite direction from that observed on marine benches, where *C. sponsalis* characteristically occupies the shoreward zone (Figs. 20-22). On the subtidal reef platform at Station 7, the bulk of the population of this species occupies the central region of the reef (Table 5). This is probably due to the infrequency of suitable substratum nearer shore, as will be discussed below.

The distribution patterns of *Conus lividus* and *C. flavidus,* two closely related species which are also similar in size, are strikingly similar, but some of the predominance of inshore individuals may be due to sampling bias.

The total density of all species is similar over most of the reef platform from shore to outer edge (Table 5). The total density decreases as the breaker line is approached, but sampling bias is also in this direction. The downward trend in the first three figures in the right hand column of Table 5 is probably not significant.

It may be concluded, then, that over most of the area of reef platforms the distribution of *Conus* is patchy, or clumped, and is not related to distance from shore or breaker line. In the zone of surf and very close to shore, however, *Conus* is less abundant, although present in low density.

SUBSTRATUM

MARINE BENCHES

By definition, a habitat must possess uniformity with respect to an important quality (Andrewartha & Birch 1954: 28). In the case of marine benches, uniformity is in the physiography of the bench platform, which constitutes the substratum of the species under consideration. This substratum is hard, rather smooth, and covered with an algal turf which may vary markedly in density. The algae, if sufficiently dense, bind sand, which is of importance because its presence increases the amount of residual water retained on the bench at low tide, and because it provides a medium into which *Conus* may burrow in order to escape desiccation or heavy wave action.

The substratum is of importance not only to adult *Conus,* but also to the pelagic veliger larvae. The importance of certain attributes of the substratum in the settling of pelagic larvae of certain other benthic marine invertebrates has been demonstrated by Wilson (1952, 1955), and this is likely to be the case in *Conus* also. Peculiarities of the substratum of marine benches may attract larvae of some species and not of others and thus determine qualitatively the species composition of the population of this habitat. The possibility of obtaining direct evidence relevant to this hypothesis was remote. However, it is probably one of a number of density-inactive mechanisms (Nicholson 1955) which determine the specific composition of populations of *Conus* on marine benches.

The hypothesis that the microhabitats of different species differed with respect to substratum preferred by the adults is more amenable to study. The predominant substratum of marine benches is the hard, algal-matted reef limestone noted above. In addition to the zonation of distribution discussed in the previous section, variations of substratum exist which may further differentiate microhabitats. These are patches of bare limestone or tuff which do not support an algal turf, and patches of sand, which usually fill shallow depressions in the bench platform. In the latter, benthic algae may or may not be present. The association of various species of *Conus* with these regions is summarized in Table 6A.

TABLE 6. Proportion of Populations of *Conus* Species Associated with Different Types of Substratum.

A. Marine Benches

Species	Sample Size	Bench with Algal Turf, Binding ± Sand		Sand Pockets or Patches on Bench		Bare Limestone or Turf	
		No.	%	No.	%	No.	%
C. sponsalis........	211	189	90%	10	5%	11	5%
C. abbreviatus.......	96	63	65%	25	26%	8	6%
C. ebraeus..........	97	63	65%	15	15%	17	18%
C. rattus...........	45	28	62%	5	11%	11	24%
C. chaldaeus........	29	13	45%	8	28%	8	28%
C. catus............	11	5	45%	2	18%	4	36%
	489	361	74%	65	13%	57	12%

B. Reef Platforms

Species	Sample Size	Sand		Reef Limestone with or without Algal Turf		Dead Coral and Coral Rubble	
		No.	%	No.	%	No.	%
C. pulicarius.......	12	12	100%	0	0%	0	0%
C. abbreviatus.......	73	57	78%	13	18%	3	4%
C. lividus..........	133	86	64%	29	22%	18	14%
C. ebraeus..........	54	33	61%	11	20%	10	19%
C. flavidus.........	130	73	56%	34	26%	23	18%
C. imperialis.......	23	11	48%	6	26%	6	26%
C. sponsalis........	61	23	38%	24	39%	14	23%
C. rattus...........	37	8	22%	14	38%	15	40%
	659	405	61%	160	25%	94	14%

C. *Conus pennaceus* on Reef Platforms

	Sample Size	SAND		Reef Limestone, with or without Algal Turf	Dead Coral and Coral Rubble
		Visible From Above	Under Rocks		
day.........	79	2	70	3	4 (all under rocks)
night........	57	30	0	26	1 (visible from above)
Total........	136	32 (102)	70	29	5
Per cent.....		75%		21%	4%

Most individuals of all species are found on the most abundant kind of substratum, algal turf on hard bench platform. A certain proportion of each species "spills over" onto the other types of substratum available. This frequency is significantly less in *Conus sponsalis* than in the other species. *C. abbreviatus* utilizes sandy areas more often than *C. sponsalis* (P< .01). *C. ebraeus* utilizes bare regions of bench more often than *C. abbreviatus*, but the difference is probably not significant (P = .08). Substratum preferences of other species do not differ significantly from one another.

The particle size distribution in samples of sand from several stations was determined by the use of graded sieves, in order to detect possible interspecific differences in preference for sand of diffrent mechanical proprties. The methods used varied but slightly from those of Holme (1954).

Since sand particles are subject to sorting by wave action, larger particles might be expected to dominate in samples taken near the outer edge of benches. Application of Wilcoxon tests to data from

Stations 5 and K4 showed that *Conus ebraeus* is associated with somewhat coarser sands than *C. abbreviatus* (P = .05). However, mechanical properties of the sand probably do not vary sufficiently to provide different microhabitats with respect to this factor.

Sandy areas are more common on reef platforms than marine benches. The small areas of sand on benches may limit the density of some species of *Conus*. *C. pennaceus* is found rarely on benches, but it is common in habitats where sand is abundant, as the animals typically remain in sand under rocks during the day. Other species of *Conus* which occur in low densities on marine benches (e.g. *C. lividus*, *C. flavidus*) may be limited indirectly by the absence of sandy substrata which are required not by them but by the species on which they prey (see section on Nature of the Food of *Conus* on Marine Benches).

REEF PLATFORMS

The predominance of a sand substratum and the absence of extensive living coral characterize the platforms of Hawaiian fringing reefs and distinguish them from those of typical atoll and barrier reefs.

The nature of the substratum associated with 659 individuals of the 9 most abundant species of *Conus* on reef platforms is summarized in Table 6B. Most of the specimens (61%) of all the species collected on reef platforms occupied sandy substrata. From 12% to 14% of the populations were found on each of the other types of available substrata: bare limestone, limestone with algal turf (combined in Table 6B), and coral (including coral rubble and dead coral). The relative abundance of the available types of substratum was not measured, but sand is by far the most prevalent. Thus, as is the case on marine benches, most of the population of *Conus* occupies the most abundant type of substratum.

Specific Differences of Substratum. Conus pulicarius is probably entirely restricted to a sandy substratum. Although the sample size in Table 6B is small, it is supported by similar unpublished data from other regions where this species occurs. *C. pulicarius* typically occurs in areas of reefs characterized by sand bottom and the absence of limestone outcrops and growing coral. Individuals are usually partly or completely buried during the day. At night, they actively crawl about through the sand, leaving a broad track which is visible from above and facilitates collection. In quiet water, these tracks are often visible the next morning, and they may lead to the discovery of completely buried individuals.

Conus flavidus and *C. lividus*, the two most abundant species on reef platforms, also occur predominantly on sand substrata but are commonest in areas of sand patches and smaller pockets among solid substratum. These two species do not differ significantly from each other with respect to the types of substratum utilized (P = .15; see Table 20). Both species are predominantly epifaunal, and individuals are rare-

ly found even partly buried in the substratum during the day.

Conus abbreviatus is also primarily a sand dweller when it occurs on reef platforms. It will be recalled that this species also occupies sandy regions of marine benches significantly more often than do the other species present. *C. abbreviatus* also burrows in sand on reef platforms significantly more often (P< .01) than the other species, with the exception of *C. pulicarius*.

The proportions of different types of substratum utilized by *Conus ebraeus* on reef platforms do not differ significantly from those of the other predominantly sand-dwelling species just discussed (Table 6B). This species is also typically epifaunal, but some individuals are found partially buried in the substratum.

Conus pennaceus is also primarily associated with a sand substratum. However, in contrast to the other species, the substratum of *C. pennaceus* is altered by the diurnal activity cycle. The substratum of 79 specimens collected during the day and 57 collected at night is shown in Table 6C. During the day, specimens are characteristically found on (37%) or partly buried in (63%) sand under basalt or coral rocks. At night, the snails actively crawl about on the surface of the sand or on reef rock, and they are visible from above. The substratum of *C. pennaceus* thus differs qualitatively from those of the other sand dwellers, which are found uncommonly under rocks.

The number of specimens of *Conus sponsalis, C. imperialis,* and *C. rattus* found on other types of substratum exceeds the number found on sand. Most of the specimens of *C. sponsalis* listed in Table 6B were collected at Station 7, where it is the most abundant species of *Conus. C. sponsalis* occurs sparsely or not at all on the other reefs studied (Figs. 14-17). The substratum of a large area of Station 7, particularly where *C. sponsalis* is common, consists of rather smooth limestone, which supports an algal turf, and dead coral, which presents a rough surface but is apparently being smoothed by wave quarrying. The former type of substratum especially is similar to that of marine benches, where *C. sponsalis* is also abundant. It is therefore not surprising that, when such a substratum is available on an otherwise predominantly sandy reef platform, it should be occupied by a population of *C. sponsalis.* Only a few scattered individuals of *C. sponsalis* are found on reefs which lack extensive areas of this type of substratum.

Conus rattus is also found more often on lithified than on sandy substrata, and in this respect probably does not differ significantly from *C. sponsalis* (P = .08). The numbers of these two species found on each of the substratum-types listed in Table 6B are significantly different, however (P = .02), in the samples collected.

Analysis of Particulate Sediments. The five most abundant species of *Conus* on subtidal reef platforms are characteristically associated with the sand moiety of the substratum. It was therefore of interest to determine the properties of the particulate sediments and the distribution of *Conus* with respect to these properties.

The sediments are almost entirely biogenic, comprising chiefly Foraminifera tests, fragments of coral, mollusk shells, echinoid tests and spines, and calcareous algae. Small amounts of olivine are often present, especially at Station 9, located at the foot of Diamond Head (Fig. 6), which takes that name from the local term "Hawaiian diamonds" for olivine.

Sediments associated with seven species of *Conus* on reef platforms were analyzed. *C. lividus* was found to be associated with somewhat coarser sediments than *C. flavidus* (Wilcoxon test: P = .05). However, all species are associated with sediments with extremely variable particle size distribution in the sand-gravel range. It therefore seems likely that, on reef platforms as on marine benches, there is no niche diversification of *Conus* species with respect to the particle size distribution of the sand moiety of the substratum.

EFFECTS OF ENVIRONMENTAL STRESSES

As Prosser (1955) has recently stated, "Determination of the importance of specific variations requires (a) the careful observation of ecological niches of subspecies and species occupying overlapping habitats, and (b) physiological tests of the effects of environmental stresses."

In order to test the effects of some environmental stresses on the species of *Conus* that inhabit marine benches, experiments on the effect of strong water currents and low oxygen tension were carried out. In addition, observations on activity with respect to desiccation will also be reported. The environment of the subtidal reef platform habitats is in general more equable than that of intertidal marine benches.

TEMPERATURE

Water temperatures ranging from 22.8 to 28.3°C were recorded at marine bench stations. The extreme range is probably somewhat greater, especially in shallow pools at low tide. Seasonal fluctuations appeared to be extremely small. Sea temperatures ranging from 22.0 to 29.1°C were measured on reef platforms. More extensive data for Station 3 were published by Edmondson (1928), who reported extremes of 21.5 and 29.0°C.

Analyses of diurnal fluctuations of temperature at Station K3 have been published elsewhere (Kohn & Helfrich 1957). On successive days in summer, ranges of 24.3-29.1°C and 24.1-27.1°C were recorded. The amplitude of diurnal temperature fluctuation thus closely approaches the annual range of variation on at least some reefs.

Temperature is not a limiting factor to species tolerant of the prevailing range, and population densities do not affect, and are not affected by, temperature. The qualitative species composition of

populations of *Conus* in Hawaii may, however, be determined at least in part by the temperature regimen. The Hawaiian Islands represent the highest latitudes at which most of the species present are known to occur. The fauna of islands at lower latitudes, where sea temperatures are higher, is richer. Some species may be excluded from the Hawaiian area by temperatures below their tolerance limits. However, most regions nearer the equator which have been studied lie closer to the Indonesia-Melanesia center of distribution, and distance from this center is also a factor of major zoogeographical importance.

Exposure to Air at Low Tide

Marine benches, but not reef platforms, are subject to periodic exposure to air at times of low tide. Therefore, only a limited range of depth of water is available on marine benches at low tide, ranging from 0 (hereafter noted as "exposed") to about a foot in tidal pools.

A certain fraction of the population of each species of *Conus* was found to be left exposed at low tide, when the bench platform may not be awash for periods of up to four hours (Table 7). The frequency of exposure is significantly higher in *C. sponsalis* than in all other species (P< .01), mainly because the sample contains the large population at Station A3, which was entirely exposed. This dense population, and the virtual absence of *C. abbreviatus*, has been noted above. *C. abbreviatus* may be unable to withstand the long periods of exposure to air required for habitation of Station A3.

TABLE 7. Proportion of Populations of *Conus* Species Exposed to Air at Low Tide.

Species	Sample Size	Number Exposed	Per Cent Exposed
C. sponsalis	144	79	55%
C. abbreviatus	83	29	35%
C. chaldaeus	31	10	32%
C. ebraeus	73	21	29%
C. catus	28	8	29%
C. rattus	47	8	17%

Data from all marine bench stations.

The low proportion of the population of *Conus rattus* which is out of water at low tide is probably due to the fact that this species occurs more often on abrasion ramp benches than on other types. Since these slope into the sea, they are more often awash at low tide than the horizontal platforms of solution benches and water-leveled benches.

All species of *Conus* observed by the writer tend to remain quiescent in the daytime. On marine benches, the algae-sand turf provides shelter from heavy wave action at high tide, when the entire bench is awash, and the residual water it retains at low tide reduces the danger of desiccation for the smaller species (*C. sponsalis, C. abbreviatus*) during the day. If the turf is dense enough and sufficient sand is

present, the shells may be completely buried. Larger species (*C. ebraeus, C. chaldaeus*) find shelter in shallow crevices or under pieces of coral rubble in the daytime.

In order to ascertain whether different species occupy different microhabitats with respect to depth of water at low tide, the proportion of each species population partly buried or otherwise sheltered was determined. The samples were rather small and excluded completely buried individuals. Nevertheless, the frequency of burrowing in *C. abbreviatus* is significantly greater than in any of the other species (P< .01). This is probably due at least in part to the preference of this species for sandier regions of the bench platform, where burrowing can be more easily accomplished. Proportions of populations of other species buried during the day did not differ significantly from each other in the samples examined.

Although seemingly unsuitable shelters that are vacant can always be found on marine benches, the density of available sheltered sites, and the ability of *Conus* to locate them when needed, may be a limiting factor of population size in some cases.

Heavy wave action, a prominent environmental factor on marine benches, is generally absent from subtidal reef platforms except near the outer edge. Large waves are broken by the outer edge of the reef, and wave action on the platform is rarely so heavy as to interfere with collecting or observation, even at high tide.

Activity Rhythms

At night, especially at low tide, the snails are typically up on the surface of marine bench platforms, moving actively about. This activity rhythm persists when *Conus* is maintained in laboratory aquaria. Degree of expansion of the foot, movement of the siphon, and movement of the entire animal are much greater at night than in the daytime, even if the aquaria are illuminated at night. Rhythmicity of activity in nature is thus probably at least partly endogenous.

Alternating periods of light and darkness are important to many marine invertebrates because they synchronize rhythms of locomotor and other activities (Brown *et al.* 1953). In the field, no interspecific differences in activity with respect to light or time of day, which might lead to reducing the possibility of interspecific competition, were noted. Enhanced activity may be correlated with the immediate presence of food, as Ohba (1952) observed in *Nassarius*, and as was shown in *Conus striatus* in the laboratory (Kohn 1956b).

The relationship of tidal fluctuation to locomotor activity in *Conus* is probably complex. Observations were hampered by the fact that most marine benches are accessible only at low tide. Maximum activity was observed during low spring tides at night. At such times, waves may not break over solution benches for periods of several hours. The retention of much residual water by the algae-sand mat and the absence

of solar radiation probably make the problem of desiccation negligible.

The initial movements of *Conus*, which begin after sunset, are mostly vertical, being directed out of the daytime hiding place up onto the bench platform. This behavior pattern is illustrated from field observations which comprised counts made in seven 100-sq ft quadrats at Station 5 at intervals over a 4-hr period in the evening. No *Conus* were visible on the bench platform at 1800 hrs, but by 2030, 17 specimens of four species had become active and were crawling about on the surface of the 700-sq ft area studied. By 2200, three additional individuals had also become active. Time of low tide (−0.2 ft) was 2023. Ohba (1952) noted activity peaks of *Nassarius* in tide pools at times when agitation of the water ceased on the receding tide and was renewed on the rising tide. In the present study, however, the bench had been exposed since before 1800. The rhythm is probably timed so that increased activity begins when two factors, darkness and absence of strongly flowing water, become favorable.

Since heavy wave action made observations on benches impossible except at low tide, experiments designed to measure the ability of *Conus* to withstand strong currents were carried out. Individuals of the four species dominant on marine benches were subjected to artificially created currents of 20, 100, 175 and 210 cm/sec. The ability to withstand the currents was found to be roughly correlated with size, in that *C. ebraeus*, which is larger than the other species (Fig. 9), is the most tenacious. The tenacity of *C. sponsalis*, *C. abbreviatus*, and *C. chaldaeus* is similar, although individuals of the last named species are somewhat larger (Fig. 9).

These data may offer a partial explanation of the observed pattern of distribution on solution benches (Fig. 20). The two smallest species are less able to withstand strong currents generated by waves breaking over the bench. By occurring chiefly on the landward portion, they are probably able to spend more time seeking food between high tides. The larger and heavier *Conus ebraeus*, on the other hand, being better able to withstand strong currents, may find a wider area of bench within its optimal habitat.

The ability of *Conus chaldaeus* to withstand strong currents in the experiments was comparable only to that of *C. sponsalis* and *C. abbreviatus*. In size, *C. chaldaeus* ranks between these species and *C. ebraeus* (Fig. 9). The experimental data thus do not help to explain the distribution pattern of *C. chaldaeus*, which characteristically occurs at the more seaward portion of marine benches. However, the data may suggest a possible explanation for the small population size of this species at Station 5, where wave action is more violent than at Station K1 and other collecting sites.

Reef Platforms. Diurnal activity cycles are difficult to observe on reef platforms. Most specimens were collected during the day, when they are typically quiescent. Little apparent difference in activity is observable in the field in the case of typically epifaunal species such as *Conus lividus* and *C. flavidus*. However, both of these species probably feed only at night, as will be shown below, and they are therefore presumably most active then.

Diurnal differences in the activity of *Conus pennaceus* are more readily observable, as alluded to in the previous section. This species is almost always found on or partly buried in sand under rocks during the day (Table 6C). At night, however, the snails leave that microhabitat to crawl about on the surface of the sand or on coral or limestone. Of 60 specimens of *C. pennaceus* collected at night, three were found crawling about out of water. Exposure to air is insignificant as an environmental stress on reef platforms, however. Exposed individuals of other species were found even more rarely or not at all.

OXYGEN REQUIREMENTS

Diurnal cycles of solar radiation and semidiurnal tidal cycles are factors leading to large fluctuations in oxygen concentration in the sea water on Hawaiian marine benches. Amplitude of fluctuation is greatest at low tide. At mid and high tides, oceanic water breaking over the bench in surf is probably always saturated. During daytime low tides residual water on the bench platform becomes supersaturated with oxygen due to photosynthesis by the dense mat of attached algae. At night low tides, oxygen content of residual water is reduced by respiration of both plants and animals.

Determinations of oxygen concentration *in situ* were made at three marine bench stations. Determinations were made by the Winkler method. The highest concentration measured was 7.68 ml O_2/l, and the lowest was 0.97 ml O_2/l, or only 19% of saturation.

It was thought that the nocturnal minimum might represent an environmental stress on *Conus*. In an attempt to determine the oxygen requirements of *Conus* and the ability to survive low oxygen tension, experiments on three of the four dominant species on marine benches were carried out in a simple respirometer. The results of three experiments, each with 14-20 specimens of *C. ebraeus*, and six experiments, each with 16-20 specimens of *C. chaldaeus*, are summarized in Fig. 23. Seven experiments with *C. abbreviatus* had erratic results, and they have not been included in Fig. 23. Indeed, all results were rather erratic, as indicated by the large standard errors. Some of this variation may be due to diurnal and tidal cycles in rate of respiration, such as have been reported in other gastropod genera by Sandeen, Stephens & Brown (1954).

The data in Fig. 23 suggest that *Conus ebraeus* and *C. chaldaeus* are probably physiological adjusters rather than regulators with respect to oxygen. That is, the rate of consumption varies with the environmental concentration rather than remaining relatively constant (Prosser 1955).

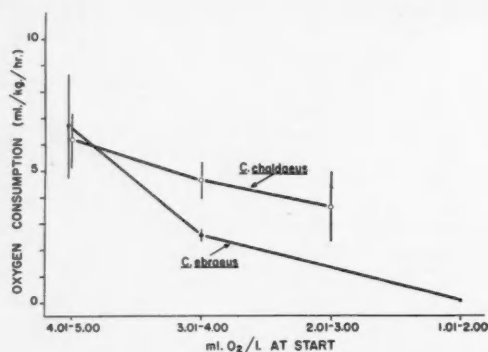Three respiratory rate determinations of *Conus*

FIG. 23. Rates of oxygen consumption of *Conus* at different oxygen concentrations. Vertical lines indicate standard error of mean.

ebraeus in water containing 1.03-1.19 ml O_2/l, near the lowest *in situ* concentration measured, showed no detectable uptake of oxygen over a period of 6 hrs. Nevertheless, all animals survived the experiment. On marine benches, oxygen concentration is probably never so low for so long a time. In addition, the typical activity cycle of *Conus* tends to obviate danger of hypoxia. When the snail crawls about out of water on the bench platform, a thin layer of water over the ctenidia ensures diffusion of oxygen from the air as the concentration in the water is reduced by passage of oxygen into the tissue.

Reef Platforms. Like temperature, oxygen concentration of the water over subtidal reef platforms undergoes diurnal fluctuation of lower amplitude than on marine benches. A graphic presentation of the diurnal cycle of oxygen concentration at Station K3 has been published (Kohn & Helfrich 1957). The minimum concentration recorded (at 0300) was 3.58 ml O_2/l, equivalent to 77% saturation. Midday values ranged to 7.27 ml O_2/l, or 168% saturation. A few determinations of oxygen concentration were also made at Stations 3, 7, and 9. The maximum value observed was 8.91 ml O_2/l (197% saturation) recorded at Station 7.

Dissolved oxygen is probably never in short supply to *Conus* on reef platforms. However, individuals of several species burrow into the sand substratum. Below a centimeter or so, these sands are usually gray. This reducing environment probably does not adversely affect *Conus*, however, since the inspiratory organ, the siphon, projects above the water-sand interface and draws a stream of oxygenated water over the ctenidia.

FOOD AND FEEDING

THE FEEDING PROCESS

Members of the genus *Conus* are known to have a unique feeding mechanism (discussed in detail by Bergh 1896, and Hinegardner 1957, 1958) and are known to be predatory (Alpers 1932a, Kohn 1955). The feeding process in piscivorous species has been de-

scribed elsewhere (Kohn 1956b). Alpers (1932b) studied the feeding process in *C. mediterraneus* Hwass in Bruguière, which feeds on polychaetes. He concluded erroneously that *Conus* ejects venom into the water in the vicinity of the prey, and he was not able to discern the function of the radula teeth.

Feeding of several of the vermivorous species which occur in Hawaii was observed in the laboratory. In *Conus abbreviatus* and *C. ebraeus*, the manner of injecting the radula tooth and accompanying venom do not differ from that described (Kohn 1956b) for *C. striatus*. However, the radula tooth is not held by the proboscis after injection. Rather, the proboscis retracts quickly, leaving the tooth in the prey. The mouth then expands and the paralyzed prey is engulfed. However, as will be noted below, other vermivorous species do retain the radula tooth within the proboscis and use it to draw the impaled prey into the mouth, as does *C. striatus*.

The method of feeding is somewhat different in *Conus pennaceus*, which, as will be shown, feeds on other mollusks. When the prey is stung, the radula tooth is completely freed from the proboscis. In contrast with the vermivorous species, not one, but up to six radula teeth may be injected into the same prey organism. If the prey is an opisthobranchiate mollusk with an internal shell, it is usually swallowed whole. The shell is presumably later regurgitated, since it is usually too large to pass into the intestine. When the prey is a prosobranch, or an opisthobranch with a large external shell, the shell is not swallowed. Rather the mouth of *C. pennaceus* is applied to the aperture of the shell of the prey after stinging. This position is maintained for 15 min-1 hr, following which the shell, now empty, falls away. Presumably the venom acts on the columellar muscle during this time, relaxing its attachment to the shell and allowing the soft body to be removed intact from the shell and swallowed. The feeding process was observed to be essentially identical in *C. textile.*

Digestion. After the prey has been completely swallowed, it lies in a large, distensible organ variously termed the crop (Clench & Kondo 1943) or esophagus (Speiseröhe of Bergh 1896; Ösophagus of Alpers 1931). Usually no digestion takes place in this organ, although enzymes may leak anteriorly from the intestine, causing some. Since there is no mechanism for trituration, prey in the esophagus is usually in a good state of preservation and identification is thus facilitated. The junction of the esophagus and intestine is marked by the entrance of two large ducts from the digestive glands. The prey is gradually moved from the crop into the intestine, where digestion and absorption occur. Fecal matter is not usually compacted into pellets but is excreted as undigested remains.

The piscivorous species represent an exception to the course of digestion just described, as noted by Kohn (1956b). Considerable digestion occurs in the anterior portion of the alimentary tract. The food swallowed is proportionally much larger than that

eaten by the other species, and the lower parts of the tract are not very distensible.

TIME OF FEEDING

Feeding takes place at night and usually not during daylight hours. This was demonstrated in the following manner. In analyses of alimentary tract contents, the position of food in the tract was recorded. Since the time of collection was noted, the position of food in the tract could be plotted against time of day. Food frequency histograms for the three dominant species on marine benches are shown for pertinent times of day in Fig. 24. Data from all marine bench stations are included. Data for three species on reef platforms are presented in Fig. 25. At other times of day (during afternoon and early evening) the proportion of snails with empty alimentary tracts was so high that it was not profitable to collect and examine large numbers of them.
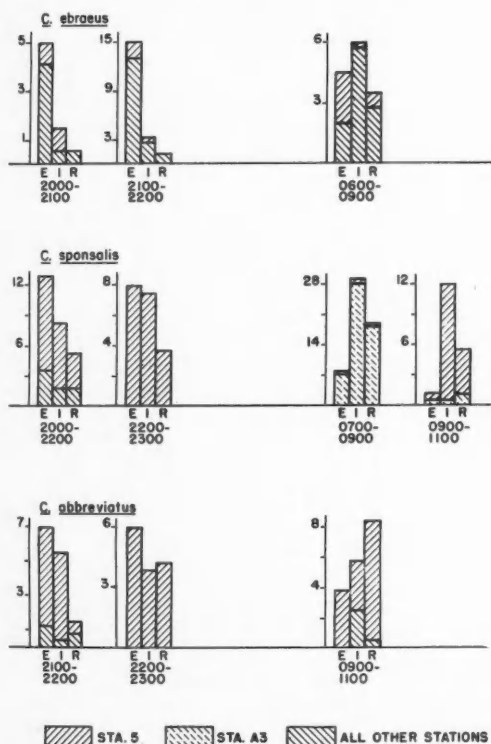
FIG. 24. Food in alimentary tracts of *Conus* collected at marine bench stations at different times of day. E = esophagus. I = intestine. R = rectum.

In Figs. 24 and 25, alimentary tracts are divided into esophagus (E), intestine (I), and rectum (R). The esophagus and intestine are quite distinct organs (Bergh 1896, Alpers 1931), while the rectum is somewhat arbitrarily considered as the region between the last curve of the intestine and the anus. The dat from marine benches show that, in all three species,
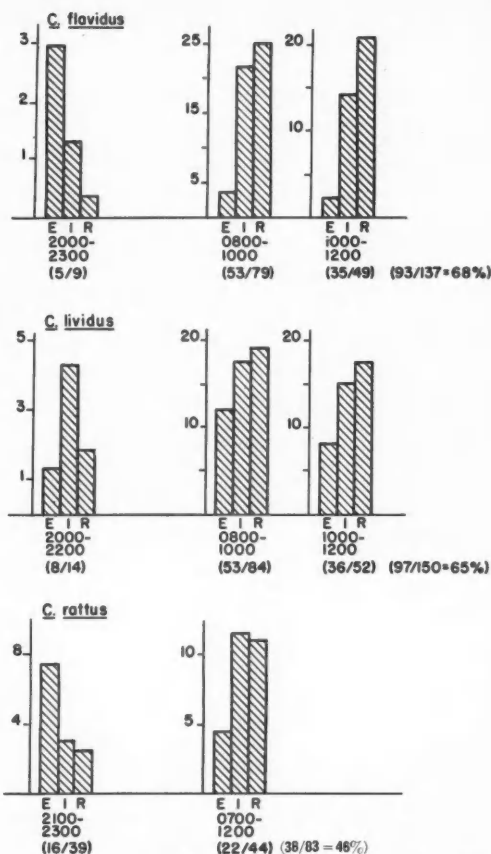
FIG. 25. Food in alimentary tracts of *Conus lividus*, *C. flavidus*, and *C. rattus* at different times of day. E = esophagus. I = intestine. R = rectum.

the crops contain the largest number of food organisms at night. By mid-morning, food has largely passed from the esophagus into the intestine and rectum, and incidence of esophagus contents is greatly reduced.

Of the dominant reef platform species, evidence of time of feeding was obtained for *Conus flavidus*, *C. lividus*, and *C. rattus*, as shown in Fig. 25. Nocturnal records for *C. flavidus* and *C. lividus* are probably too few to be meaningful. That feeding takes place at night in *C. flavidus* is plainly shown, however, by the low incidence of prey in the esophagus during the day. In *C. lividus*, the data are less clear-cut. This may be due to a slower rate of digestion, or some feeding may take place during daylight hours. *C. rattus* is plainly a nocturnal feeder. At night, prey organisms are found chiefly in the esophagus, while during the morning their remains occupy the lower regions of the alimentary tract.

The number of specimens examined which had food in the alimentary tracts is also indicated in Fig. 25. About two-thirds of the population of both *Conus*

TABLE 8. Prey Organisms Consumed by Vermivorous Species of *Conus* at Marine Bench Stations

	sponsalis				abbreviatus		ebraeus			chaldaeus			rattus	lividus			flavidus		miles	distans
Station...	5	11	A3	T	5	T	5	11	T	5	11	T	T	5	11	T	5	T	T	T
No. Specimens Examined	45	51	92	258	158	243	94	5	122	25	12	59	79	10	1	24	6	10	1	2
Nereis jacksoni Kinberg var.	—	6	5	30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Perinereis helleri Grube	15	14	—	32	19	20	104	3	115	—	—	—	13	—	—	—	—	—	—	—
Platynereis dumerilii (Audouin & Edwards)	2	2	6	10	2	3	—	—	—	17	16	45	—	—	1	1	—	—	—	—
Nereid sp. 350	1	2	1	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Nereidae	—	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Nereidae	18	24	13	77	22	24	104	3	115	17	16	45	13	—	1	1	—	—	—	—
Lysidice collaris Grube	2	3	3	11	5	27	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Palola siciliensis (Grube)	—	—	—	—	—	—	3	3	7	4	—	8	—	—	—	—	—	—	—	—
Eunice antennata Savigny	—	1	1	2	1	2	—	—	—	—	—	—	12	—	—	—	—	—	—	—
Eunice (Nicidion) cariboea (Grube)	—	5	30	36	8	10	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Eunice filamentosa Grube	1	—	—	1	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Marphysa sanguinea (Montagu)	—	—	1	1	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eunice afra Peters	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Unidentified Eunicidae	1	—	—	1	1	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Lumbrinereis sarsi (Kinberg)	2	3	8	14	10	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arabella iricolor (Montagu)	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Eunicea	6	12	43	66	28	61	3	3	8	4	—	8	13	—	—	—	—	—	1	1
Nicolea gracilibranchus (Grube)	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	4	2	—	—	—
Terebellid sp. 837	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—
Cirriformia semicincta (Ehlers)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Polydorid sp. 1500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Unidentified annelids	—	1	3	6	4	4	1	—	1	—	—	—	—	—	—	2	1	—	—	—
Total Annelids	24	36	59	149	45	89	108	6	124	21	16	53	26	1	1	8	—	7	1	1
Total Identified Food	24	36	59	149	54	89	108	6	124	21	16	53	26	3*	1	16†	—	7	1	1
Unidentified Food	1	1	1	4	1	3	—	—	—	—	—	—	—	—	—	3	—	1	—	—

Data from Stations 5, 11, and A3 are entered separately as noted.   T = Data from all bench stations.
Numbers in body of table indicate numbers of polychaete species at left found in alimentary tracts of *Conus* species at top.
Chief references used in the identification of the polychaetes were Abbott (1946), Hartman (1940, 1944, 1948), Holly (1935), Fauvel (1927), Okuda (1937), and Treadwell (1906, 1922).
*Includes one specimen definitely identified, and one tentatively identified, as *Ptychodera flava laysanica* Spengel.
†Includes five specimens definitely identified, and three tentatively identified, as *Ptychodera flava laysanica* Spengel.

flavidus and *C. lividus,* and about one-half of the population of *C. rattus* succeed in capturing food each night.

Investigation of the rate of passage of food through the alimentary tract of *Conus abbreviatus* showed that the food starts passing into the intestine after about 1.5 hrs in the esophagus. After about 3 hrs, fecal matter is present in the rectum. From 12–24 hrs after feeding, the alimentary tract is completely emptied. Therefore, gastropods observed with empty tracts in the afternoon may or may not have fed the previous night.

NATURE OF THE FOOD OF *Conus* ON MARINE BENCHES

Solution Bench Stations. Of the eight species of *Conus* present at Station 5, five, including the four dominant species, were found to feed exclusively on polychaete annelids. Of the less abundant species, *C. flavidus* feeds predominantly on polychaetes but may occasionally take an unsegmented worm. *C. lividus* feeds on the enteropneust *Ptychodera flava* but consumes polychaetes as well. *Ptychodera* is a sand-dwelling worm and is uncommon on marine benches. Both *C. flavidus* and *C. lividus* prefer Terebellidae among the polychaetes. These worms are also typically sand dwellers, building tubes on the sides of rocks partly buried in sand. The low abundance of *Ptychodera* and terebellids on benches may limit the populations of *C. lividus* and *C. flavidus* in this habitat.

Conus pennaceus was earlier reported (Kohn 1955) to feed on other gastropods. Small species of the type on which *C. pennaceus* thrives (especially *Haminoea*) are abundant on benches, so the low

density of *C. pennaceus* does not seem the result of limited food supply. Rather, *C. pennaceus* is probably limited by lack of sufficient sand in which to burrow during the day.

Contents of alimentary tracts of 343 specimens collected at Station 5 were determined by dissection of fixed specimens or collection of fecal matter from living individuals. From these, 210 prey organisms were identified, 199 of them to species. All eight species of *Conus* are represented in the sample, but food remains were not found in any alimentary tracts of the few *C. rattus* and *C. pennaceus* examined. The results are summarized in Table 8, which also includes totals from other bench stations for comparison.

These data show that at Station 5, *Perinereis helleri* is the primary food of the three most abundant species of *Conus*. *C. ebraeus* eats this species almost exclusively, while *C. abbreviatus* especially feeds on other polychaetes as well. Members of the superfamily Eunicea (only the families Eunicidae, Lumbrinereidae, and Arabellidae are represented) are eaten about as often as nereids. *C. sponsalis,* on the other hand, is more restricted to nereids. This may reduce the possibility of competition for food between these two species, which feed in the same zone of the bench. Most of the population of *C. ebraeus* is found feeding in the central portion of the bench (Fig. 20) and is thus seeking *P. helleri* in a different place from *C. sponsalis* and *C. abbreviatus.*

The food of the fourth commonest species, *Conus chaldaeus,* is strikingly different. *C. chaldaeus* also feeds exclusively on a single species of nereid, but its food is *Platynereis dumerilii,* which occurs predominantly toward the outer edge. A large substratum sample collected near the outer edge at Station 5, adjacent to two specimens of *C. chaldaeus,* contained the following Nereidae:

Platynereis dumerilii	16
Nereis jacksoni	14
Perinereis helleri	1
Unidentified epitokes	3

Thus *P. dumerilii* is an order of magnitude more abundant than *P. helleri* near the outer edge. The prey species of *C. chaldaeus* is thus correlated with the distribution pattern across the reef platform, as both prey and predator are less abundant near shore.

The three most abundant species of *Conus* exert an active demand on the local population of *Perinereis helleri.* If this demand were found to exceed the immediate supply of the prey species, it could be said that the three predator species compete with each other for this food, at least in areas of distribution overlap.

Food organisms were found in about 60% of all alimentary tracts of specimens examined from Station 5. Since specimens were collected at all hours, and since feeding has been shown to take place only at night, it is possible that some individuals had defecated remains of the previous night's meal before being examined. A mean of one polychaete per

gastropod per night is a reasonable estimate of feeding rate.

The mean density of the *Conus* species that feed on *Perinereis helleri* is 2/100 sq ft. Since *P. helleri* constitutes about 74% of their diet, these species consume an average of 1.5 individuals of *P. helleri/* 100 sq ft/night, or $0.17/m.^2$/night. Substratum samples taken about halfway across the bench contained the densities of nereids shown in Table 9. At the calculated feeding rate, about 28 years would be required to exhaust the observed population of *P. helleri,* considering no replacement.

TABLE 9. Population Density of Nereidae and Eunicea Halfway Across Station 5.

Species	No. counted in 625 cm.^{2}	No./m.^{2}	Eaten by *Conus* /m.^{2}/day
Perinereis helleri....	121	1,940	0.17
Nereis jacksoni......	267	4,270	
Platynereis dumerilii.	7	112	
All Eunicea.........	4/30 cm.^{2}	1,300	

Although the smaller *Nereis jacksoni* was more abundant than *Perinereis helleri* at Station 5, it was not found to be eaten by *Conus.* Elsewhere it is eaten by *C. sponsalis* (Table 8).

The feeding habits of the species at Station 11 are shown in Table 8 to be essentially similar to those at Station 5. In addition, the few specimens of *Conus rattus* collected there were found to consume both nereid and eunicid polychaetes. The single specimen of *C. catus* collected had an empty alimentary tract.

No quantitative samples of polychaetes at Station 11 were analyzed. However, *Perinereis helleri* was observed to be common. Each of two samples, representing a few square centimeters of substratum surface, contained 9 polychaetes, of which 3 and 5, respectively, were *P. helleri.* Standing crop is probably of the same order as at Station 5.

Water-leveled Bench Stations. Alimentary tracts of 92 specimens of *Conus sponsalis* from Station A3 were analyzed. Of these, 90 were collected between the hours 0700 and 0900. Polychaete remains were found in 55 specimens. The frequency distribution of remains in alimentary tracts is shown in Fig. 24. The low frequency of esophagus contents indicates that feeding had ceased some time before collection, probably at or before dawn. Most of the remains are seen to be in the intestine and/or rectum. This is in essential agreement with data from other stations.

Fifty-two of the specimens examined contained remains of one polychaete in each, two contained remains of two polychaetes each, and one contained remains of three polychaetes. It may be concluded that most individuals succeed in capturing one polychaete per night.

The nature of the food of *Conus sponsalis* at Station A3, shown in Table 8, differs markedly from that

of other bench stations. The primary prey organism is not a nereid, but the eunicid, *Eunice (Nicidion) cariboea*. *Perinereis helleri* was not found to be eaten at all (but its presence at Station A3 was not ascertained). This resulted in eunicids far exceeding nereids in the prey of *C. sponsalis* at Station A3, in contrast with other stations studied. This may be correlated with the fact that *C. abbreviatus*, which generally (Table 8) feeds on eunicids more often than nereids, is virtually absent from Station A3. It may be conjectured that where the two co-occur, they compete for eunicids, with the result that *C. abbreviatus* is the more successful, and *C. sponsalis* is forced to eat nereids, which are possibly less desirable as food. When *C. abbreviatus* is excluded for other reasons from a microhabitat where *C. sponsalis* does occur, the latter species would then be able to exploit eunicids as food.

As for other polychaete feeders at Station A3, remains of *Eunice antennata* were found in three of the seven specimens of *Conus rattus* which were examined, and the single *C. abbreviatus* had fed on a *Lysidice collaris*.

The food of *Conus catus* has previously been shown to be small fishes, chiefly blennies and gobies, and the feeding process has been briefly described (Kohn 1956b). Remains of fishes were found in two of the three specimens collected at Station A3. One of the fishes was identified as the goby, *Bathygobius fuscus*. The other was too poorly preserved to permit identification. The food of *C. catus* at bench stations is summarized in Table 10.

TABLE 10. Prey Organisms Consumed by *Conus catus* at Marine Bench Stations.

	Sta. Kl	All Bench Stations
No. Specimens Examined.....	13	24
Bathygobius fuscus (Rüppell)..	2	3
Istiblennius gibbifrons (Quoy and Gaimard)............	3	3
Unidentified fishes...........	2	5
Total Fishes..............	7	11
Unidentified fecal matter.....		1

Only small samples of most species from Station K1 were examined for alimentary tract contents. The expected prey organism, *Perinereis helleri*, dominated in *Conus sponsalis* and *C. ebraeus*. Nine of 10 food organisms isolated from *C. abbreviatus* were *Lysidice collaris*. Thirty-eight specimens of *C. rattus* were analyzed. Eleven contained remains of *P. helleri*, one, *Eunice antennata*, and the remaining 26 were devoid of identifiable food. Results of analysis of alimentary tracts of 13 specimens of *C. catus* are shown in Table 10. The single specimen of *C. retifer* was found to have an empty alimentary tract. However, other members of its subgenus (*Cylinder*) feed exclusively on other gastropods, and it is likely that *C. retifer* does also.

Polychaetes did not appear as abundant as on solution benches, but no quantitative samples were collected. *Perinereis helleri* and *Lumbrinereis* sp. 239 were observed to be present. Three of the eight species of *Conus* collected feed primarily on *P. helleri*. It is not known whether the demand exceeds the immediate supply and, therefore, whether food is the requisite which governs population size. The possibility of competition for food between *C. catus* and the other species present is entirely precluded, as it feeds on fishes.

FOOD PREFERENCE

Of the species of *Conus* characteristic of the marine bench habitat, *C. sponsalis* and *C. abbreviatus* have been shown to be most similar to each other with respect to feeding habits and pattern of distribution. Both species feed exclusively on polychaetes. Frequency of different prey species found in alimentary tracts is shown in Table 8. If data from all marine benches studied are combined (Column T), polychaetes of the superfamily Eunicea comprise 68%, and Nereidae 26% of the diet of *C. abbreviatus*. The diet of *C. sponsalis* consists of 44% Eunicea and 52% Nereidae. Although feeding habits are rather similar, the difference between the two species is significant $(P = 10^{-3})$ in the samples analyzed.

Polychaetes of both groups are abundant (Table 9). The observed differences in feeding frequency may be accounted for by two alternative hypotheses: (1) *C. abbreviatus* is better adapted to feeding on eunicids, which burrow into limestone and coral, than on nereids, which occur epifaunally among the holdfasts of algae. Conversely, *C. sponsalis* is better adapted to feeding on nereids than eunicids. (2) *C. abbreviatus* exhibits active preference for eunicids over nereids, and *C. sponsalis* prefers nereids to eunicids.

Comparison of results of food studies at Station A3 with other stations provided at least some evidence in favor of the view that, where the two species co-occur, *C. abbreviatus* is the more efficient predator on eunicids.

The second hyopthesis was tested experimentally in a choice chamber, following the method of Van Dongen (1956). The chamber was a lead-sheathed wooden sea water table 125×58 cm in area and 8 cm deep (Fig. 26). Polychaetes were placed in Bull Durham bags, which were secured to the chamber floor. The water current thus passed over the polychaetes and then over the snails. All stimuli received by *Conus* from the polychaetes were thus of a chemical nature. Actual predation was prevented by the cloth bags, from which snails were unable to extract the polychaetes. In each experiment, one or two polychaetes were placed in each bag, and 12-59 specimens of a single species of *Conus* were placed at a distance of 88 cm from the goal (Line cd, Fig. 26).

Experiments were usually begun in late afternoon and allowed to continue overnight, to coincide with the snails' normal food-seeking regimen. A few of
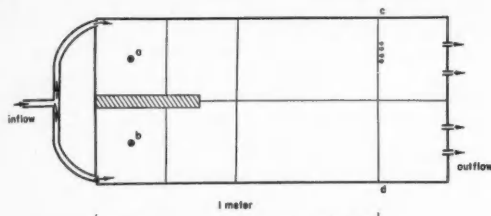
FIG. 26. Choice chamber for determination of food preferences of *Conus*. Lines were marked on floor of chamber as shown. During an experiment, fresh sea water was admitted to the chamber equally through the two inflow tubes. Outlets were located 1 cm above the chamber floor, so that a uniform depth of 1 cm of water was maintained in the chamber. A wooden partition (hatched) 40 cm in length partially separated the two portions of the chamber. This served to prevent mixing of stimuli and alteration of choice by snails. Food chambers are shown at a and b. Line cd is the starting line along which snails were placed at outset of an experiment.

the experiments with *Conus sponsalis* were allowed to run 40 hrs. At the termination of an experiment, snails were scored as having reached to within 25-50 cm of the goal, less than 25 cm, or adjacent to the food chamber. In the summary of results (Table 11), all three categories are summed.

TABLE 11. Summary of Results of Food Choice Experiments with *Conus sponsalis* and *C. abbreviatus*.

Number of Experiments	Number of Snails	Nereidae* Chosen	Eunicidae Chosen
C. sponsalis			
6	222	42	28**
2	61	22	2***
Total 8	283	64	30
C. abbreviatus			
2	87	17	35**

Figures in body of table indicate number of snails choosing polychaete listed above in choice chamber experiments.
* = *Perinereis helleri*
** = *Eunice antennata*
*** = *Palola siciliensis*

Table 11 shows that, given equal choice of both, *Conus abbreviatus* chooses the eunicid (*Eunice antennata*) more often than it chooses the nereid (*Perinereis helleri*). *C. sponsalis* chooses the nereid (*P helleri*) more often than either of the eunicids tested (*E. antennata, Palola siciliensis*). The difference in preference for eunicids and nereids between *C. sponsalis* and *C. abbreviatus* is highly significant (P < .01).

Comparison of Food in Nature and Choice Experiments. A comparison between the experimental choices and food in nature is made in Table 12. Since the percentages given do not permit direct comparison between the experiments and nature, the ratios of eunicids to nereids for *Conus abbreviatus* and *C. sponsalis* are included. Variation of the relative frequency of predation on nereids and eunicids in nature from the frequency of choice in the experiments is

significant for *C. sponsalis* (P = .05) but not for *C. abbreviatus* (P ≫ .1).

TABLE 12. Comparison of Results of Choice Chamber Experiments with Food Habits of *Conus sponsalis* and *C. abbreviatus* in Nature.

	Food in Nature (all marine benches)	Choice in Experiments
C. sponsalis		
Nereidae......	52%	23%
Eunicea.......	44%	11%
Ratio E:N.....	1:1.3	1:2.1
C. abbreviatus		
Nereidae......	26%	20%
Eunicea.......	68%	40%
Ratio E:N.....	2.6:1	2.0:1

Comparison of data for nature and experiments shows that the food of *Conus sponsalis* and *C. abbreviatus* in nature is reflected in the choice experiments. The partition of the environment into different but overlapping microhabitats which occurs with respect to food may therefore be maintained by active preference of different prey species by the two predator species.

The hypothesis that *Conus sponsalis* is better adapted to feeding on nereids than eunicids was not amenable to experimental test. It has been suggested, however, that information bearing on this question might be gained from study of radula morphology (Peile 1939).

Although the anterior extremities of radula teeth show considerable variation throughout the genus *Conus*, the teeth may be grouped in two categories with respect to the posterior portion, or base. In the first, the base is simple and of more or less greater diameter than the shaft, thus forming a terminal knob. The base in the second group is characterized by the presence of a forward projecting cone (Fig. 27).

FIG. 27. Radula tooth of *Conus abbreviatus*. The forward projecting cone is visible at the left.

Peile (1939) made the plausible suggestion that this cone might serve to retain the tooth within the proboscis when prey is attacked. It was shown, however, that *C. striatus* which does not possess such a cone, retains the tooth in the proboscis in feeding (Kohn 1956b).

It will be shown below that the presence of the forward projecting cone is generally correlated with feeding on eunicid and other tube-dwelling polychaetes in nature. Eunicids, unlike nereids, live in burrows in coral and reef rock, and the basal cone may well aid the predator in extracting the worm from its burrow.

TABLE 13. Prey Organisms Consumed by Vermivorous Species of *Conus* at Subtidal Reef Stations. Numbers in body of table indicate number of polychaete species at side found in alimentary tracts of *Conus* species at top.

	sponsalis			abbreviatus				ebraeus				chaldaeus		miles		rattus			distans	
Station	7	R	T	3	9	R	1	3	9	R	T	R	T	R	T	15	R	T	R	T
No. specimens examined	64	72	330	19	24	99	342	15	8	55	199	4	106	11	20	18	55	149	19	21
Nereis jacksoni Kinberg var.	4	4	34	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Perinereis helleri Grube	3	3	35	—	—	—	20	—	1	6	136	—	5	—	—	7	7	21	—	—
Platynereis dumerilii A. & E.	3	3	13	—	—	—	3	—	—	—	—	2	98	—	—	—	1	1	—	—
Nereid sp. 350	1	1	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Nereidae	1	1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Nereidae	12	12	89	—	—	—	24	—	1	6	136	2	103	—	—	7	8	22	—	—
Lysidice collaris Grube	6	6	17	—	—	9	36	—	—	2	2	—	—	5	16	—	—	—	—	—
Palola siciliensis (Grube)	—	—	—	—	—	1	1	14	8	29	44	—	14	—	—	—	—	—	—	—
Eunice antennata Savigny	1	1	3	5	10	20	22	—	—	—	—	—	—	1	1	3	17	29	1	1
Eunice (N.) cariboea Grube	—	3	39	—	—	—	4	—	—	1	1	—	—	—	—	1	1	2	—	—
Eunice afra Peters	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	9	9	12	13
Marphysa sanguinea Montagu	—	—	1	1	1	3	6	—	—	—	—	—	—	—	—	—	—	—	—	—
Eunice filamentosa Grube	—	—	1	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Eunicidae	—	—	1	1	—	1	2	—	—	—	1	—	1	—	—	—	—	—	—	—
Lumbrinereis sarsi (Kinberg)	2	3	17	—	—	—	11	—	—	—	—	—	—	—	—	—	—	—	—	—
Arabella iricolor (Montagu)	—	—	—	—	—	5	9	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Eunicea	9	13	79	8	11	43	104	14	8	32	48	—	15	6	17	8	27	40	13	14
Eurythoe complanata (Pallas)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Annelids	1	1	7	—	—	—	4	—	—	1	2	—	—	—	—	—	—	—	—	—
Total Annelids	22	26	175	8	11	43	132	14	9	39	186	2	118	6	17	15	35	62	13	14
Total Identified Food	22	26	175	8	11	43	132	14	9	39	186	2	118	6	17	15	35	62	13	14
Unidentified Food	2	2	6	—	—	—	4	—	—	—	—	—	1	—	—	—	—	—	1	1

SUMMARY OF FOOD OF *Conus* IN

THE MARINE BENCH HABITAT

Conus abbreviatus and *C. sponsalis,* both of which possess the small cone at the base of the radula tooth, feed on polychaetes which belong to different groups, the Nereidae and Eunicea, and differ ecologically as noted above. Although there is overlap (63%), the difference in numbers of the two groups of prey organisms eaten by *C. abbreviatus* and *C. sponsalis* is highly significant ($P = 10^{-3}$). Comparison by individual species of the food eaten by these two *Conus* species on all bench stations (Table 8) revealed overlap of only 25% and the probability of only 10^{-6} that the polychaetes preyed on represented random samples from the same population. Differences between the species composition of the food of *C. sponsalis* and *C. abbreviatus* are thus sufficiently great that competition for food is unlikely.

Of the other species which occur in the marine bench habitat, *Conus ebraeus* and *C. chaldaeus* do not possess the forward projecting cone on the radula tooth. Both species are extremely oligophagous. Nereids comprise 85% of the food of *C. chaldaeus* and 93% of the food of *C. ebraeus*. The two species do not differ significantly in the proportion of the diet comprised by nereids ($P = .24$). In striking contrast to this, however, is the specific nature of the prey eaten, as shown in Table 8. In the samples collected on all marine benches, the only nereid eaten by *C. ebraeus* was *Perinereis helleri*, while the only nereid eaten by *C. chaldaeus* was *Platynereis dumerilii*. Despite the fact that both predators are typically found on the same benches, and with overlapping distributions, they were never found to eat the "wrong" polychaete in the bench habitat.

Unfortunately, no choice experiments were carried out in order to test the possibility of differences in active preference of prey species by *Conus ebraeus* and *C. chaldaeus*. It is likely that the specific differences in prey are correlated with differences in the ecology of the prey species. In Table 9 *Perinereis helleri* was shown to be two orders of magnitude more abundant than *Platynereis dumerilii* about halfway across the bench at Station 5, where *C. ebraeus* is maximally abundant. Nearer the outer edge, where *C. chaldaeus* reaches its peak density, *P. dumerilii* is an order of magnitude more abundant than *P. helleri*.

R = All reefs; T = All stations; * = All from Station 4; + = Equals Total.

vexillum			*vitulinus*	*imperialis*	*pulicarius*		*flavidus*				*lividus*					
9	R	T	T*	R+	9	R+	3	9	R	T	3	7	9	R	T	Station
13	16	17	4	31	11	20	47	56	182	192	32	46	34	216	240	No. Specimens Examined
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*Nereis jacksoni* Kinberg var.
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*Perinereis helleri* Grube
—	—	—	—	—	—	—	—	—	—	—	1	5	—	11	12	*Platynereis dumerilii* A. & E.
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Nereid sp. 350
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Unidentified Nereidae
—	—	—	—	—	—	—	—	—	—	—	1	5	—	11	12	Total Nereidae
—	—	—	—	—	2	2	5	5	24	24	—	—	—	—	—	Capitellid sp. 1040
—	—	—	—	—	—	—	—	—	11	11	—	—	—	—	—	*Thelepus setosus* Quatrefages
6	9	9	—	—	—	—	13	5	22	22	—	—	—	1	1	*Polycirrus* sp. 660
—	—	—	—	—	—	—	—	—	2	5	—	—	1	1	1	Terebellid sp. 837
—	—	—	1	—	—	—	10	17	32	34	2	—	—	7	11	*Nicolea gracilibranchus* (Grube)
5	6	6	—	4	—	—	—	—	—	—	2	—	—	1	2	Unidentified Terebellidae
—	—	—	—	—	—	—	23	22	67	72	2	—	1	10	15	Total Terebellidae
—	—	—	—	—	—	—	—	—	5	5	—	—	—	1	1	Polydorid sp. 1500
—	—	—	—	—	—	—	—	—	1	1	—	1	1	4	5	*Cirriformia semicincta* (Ehlers)
11	15	15	1	4	—	—	—	—	—	—	—	—	—	2	2	*Lygdamis nesiotes* (Chamberlin)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3	*Sabellastarte indica* Savigny
—	—	—	—	11	—	—	1	3	4	5	—	1	—	2	3	Unidentified Annelids
11	15	15	1	15	—	—	29	30	101	108	3	7	2	33	41	Total Annelids
—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	*Thalassema* sp.
—	—	—	—	—	—	—	1	—	1	1	13	5	8	28	33	*Ptychodera flava laysanica* Spengel
—	—	—	—	—	—	—	—	—	1	4	2	5	6	29	32	*P. flava laysanica* Spengel (tentative identification)
—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	*Octopus* sp.?
11	15	15	1	15	2	4	30	30	106	113	18	17	16	90	106	Total Identified Food
2	—	2	1	2	—	3	7	5	18	21	5	10	6	39	42	Unidentified Food

Conus rattus, the other vermivorous species characteristic of marine benches, does possess the basal cone on the radula tooth. It feeds predominantly on eunicids (Table 8) and in the proportion of Eunicea eaten does not differ significantly from *C. abbreviatus*. However, the specific nature of the food of these two species is significantly different ($P = 10^{-6}$). In fact, the nature of the food of each vermivorous species of the marine bench habitat differs significantly from that of all others at the 1% level. Thus these species, as well as *C. catus* which eats only fishes, avoid interspecific competition for food in the bench habitat.

NATURE OF THE FOOD OF CONUS ON SUBTIDAL REEFS

Of the 16 species of *Conus* collected by the writer on reef platforms, 10 were found to feed exclusively on polychaetes. These are *C. abbreviatus*, *C. ebraeus*, *C. sponsalis*, *C. rattus*, *C. imperialis*, *C. chaldaeus*, *C. vexillum*, *C. distans*, *C. vitulinus*, and *C. miles*. Polychaetes constitute more than 90% of the food of *C. flavidus*, which occasionally consumes an unsegmented worm. Polychaetes comprise about 50% of the food of *C. lividus*, which feeds also on an entero-

pneust. *C. pulicarius* feeds on polychaetes and echiuroids, as far as is known. *C. pennaceus* and *C. marmoreus* feed on other gastropods, and *C. striatus* feeds on fishes.

VERMIVOROUS SPECIES

Species Typical of Marine Benches Which Occur also on Reef Platforms. The species composition of the food of the vermivorous species of *Conus* which occur on reef platforms is given in Table 13 for a sample of 784 specimens of 13 species. From these, 360 prey organisms were identified, 254 of them to species. Most of the records are determinations of alimentary tract contents of fixed specimens. A few represent collection of fecal matter from living individuals. Total data for certain species include records from marine bench and deep water habitats for comparison.

The more diversified food on reefs in comparison with marine benches is made possible by the addition of the sand substratum microhabitat on reef platforms. All of the prey species listed in Table 13 but not in Table 8 are associated with the sand substratum. All but one of the polychaetes eaten by

Conus on marine benches were found to be present and eaten on reef platforms. The limestone outcrops and coral of the reefs provide abundant burrowing sites for eunicids. Nereids, however, are not common on the reefs, except where an algal turf is present on exposed limestone. This is especially reflected in the feeding habits of *C. sponsalis*, *C. abbreviatus*, *C. ebraeus*, and *C. rattus*. *Perinereis helleri* is the dominant prey of each of these species on marine benches (Table 8), but it is much less important to all four on reefs, where it is less abundant.

On reef platforms, *Conus sponsalis* is often found in regions of dead coral and reef limestone which support an algal turf and nereids, as well as eunicids. Both groups of polychaetes are eaten by *C. sponsalis*, in frequencies which do not differ significantly from those eaten by marine bench populations of this species.

No nereids were found in alimentary tracts of 99 specimens of *Conus abbreviatus* collected on coral reefs. This is as expected, since on reef platforms *C. abbreviatus* is not found on the algae-matted areas where some nereids occur. Eunicea, which commonly burrow into any available limestone on coral reefs (Hartman 1954), apparently constitute the entire diet of *C. abbreviatus*. The frequency of different polychaete species eaten differs significantly between bench and reef populations of *C. abbreviatus*. This is due largely to the predominance of *Eunice antennata* as prey in the latter habitat.

The food of *Conus ebraeus* in reef habitats also varies from that on marine benches in the direction of increased concentration on a species of eunicid. In contrast with the previous species, however, *C. ebraeus* feeds chiefly on *Palola siciliensis* and does not eat *Eunice antennata*.

The most obvious difference between the ecological niches of *Eunice antennata* and *Palola siciliensis* is that the latter species is typically found in more dense limestone. This observation is correlated with the fact that the mandibles are larger and stronger in *Palola* than in the other genera of Eunicea. (This has been discussed by Hartman (1954), who suggests that *Palola* may be the most destructive of the Eunicea to coral reefs. Following the same criterion, *Lysidice*, *Eunice*, *Marphysa*, *Lumbrinereis*, and *Arabella* would follow in order of decreasing destructiveness.) Filamentous algae were observed in intestines of *E. antennata*. These are perhaps the boring forms recently discussed by Odum & Odum (1955). The food of *P. siciliensis* was not determined. Takahashi (1939) concluded that several eunicids inhabiting coral reefs are omnivorous, consuming sand, diatoms, crustaceans, and algal fragments.

Conus chaldaeus occurs rather rarely on reef platforms. *C. rattus*, on the other hand, is about as common as it is on marine benches. As in other species common to both habitats, eunicids are consumed significantly more often than nereids (P = .03) by reef than bench populations of *C. rattus*.

In summary, there is virtually no qualitative difference in the specific nature of the prey eaten by those species of *Conus* common to both the reef and bench habitats. The frequencies of the different species eaten vary considerably, however, and are correlated with differences in substratum characteristics of the two habitats.

Typical Reef Platform Species. The most abundant species of *Conus* on subtidal reef platforms were shown (Figs. 14-17, 19) to be *C. flavidus* and *C. lividus*. Prey organisms recovered from alimentary tracts of about 200 specimens of each of these species are listed in Table 13. It is readily apparent that *C. flavidus* feeds almost exclusively on polychaetes, that the largest single item in the food of *C. lividus* is the enteropneust, *Ptychodera flava*, and that these species feed only occasionally or never on nereids and eunicids.

Tubicolous polychaetes comprise almost the entire diet of *Conus flavidus*. About two-thirds of these are members of the family Terebellidae. The other main prey species is an unidentified species of the family Capitellidae. The terebellids on which *C. flavidus* feeds live in tubes which are usually attached to the under sides of coral rocks or pieces of rubble resting in sand. The intestines of these polychaetes are usually filled with extremely fine sand particles. The terebellids are probably selective deposit feeders, selection apparently being effected by the tentacles.

Conus flavidus consumes enteropneusts only occasionally. In contrast, *Ptychodera flava* constitutes about 50% of the diet of *C. lividus*. Since it has no hard parts, *P. flava* is particularly difficult to identify in the partially digested state. The reddish eggs, which are apparently refractory to the digestive enzymes of *Conus*, aided identification of the females eaten. However, a number of *C. lividus* alimentary tract contents, which appeared to be remains of *Ptychodera*, could not be positively identified. These are entered separately in Table 13, but they are included in "total identified food."

The ecological niche of *Ptychodera flava* differs markedly from those of the terebellids on which *Conus lividus* feeds less often. Although all are deposit feeders in the same habitat, *P. flava* moves slowly about through the sand. It appears to be a nonselective feeder, ingesting in the manner of an earthworm. A wide range of sand particle sizes is found in its alimentary tract. As there is no apparent mechanism for trituration, the particle size distribution in the tract is presumably identical with that of the environment, but this was not determined.

The feeding of *Conus lividus* on *Ptychodera flava* was observed in the laboratory. When both were placed in a dish of sea water, the rostrum, but not the proboscis, of *Conus* was extended. When the mouth touched the worm, the latter was engulfed without being stung. During the entire engulfment process, which lasted only about 15 sec, the *Ptychodera* continued its normal peristaltic pulsations. This method of feeding may not be duplicated in nature. The observed presence of radula teeth in the ali-

mentary tract with food remains indicates that *C. lividus* stings *Ptychodera* as well as polychaetes before feeding.

Other Reef Species. The remaining six reef-inhabiting vermivorous species together comprise only about 6% of the total population of *Conus* in this habitat. It was possible to collect and analyze only small samples, but the results obtained are of considerable interest and are included in Table 13 for completeness.

The most common of these species is *Conus imperialis*. Only two prey species were found in analyses of alimentary tract contents and recovery of fecal matter of 31 specimens. One of these was the eunicid, *Marphysa sanguinea*, which is also eaten to some extent by other species of *Conus*. Notes on the ecology of this polychaete were recorded by Abbott (1946), who stated that "this species has been found only in limited areas of the pond [Wailupe Fish Pond, Oahu] where the bottom is sandy and the salinity close to that of sea water. Here it occurs under rocks, and does not appear to burrow deeply into the sand. It has not been found in regions where a soft mud bottom prevails."

The more common prey of *Conus imperialis* is the amphinomid polychaete *Eurythoe complanata*. Although this species is the most conspicuous polychaete on Hawaiian coral reefs, it was never found to be eaten by any other species of *Conus*. *Eurythoe* possesses extremely abundant large setae, which easily penetrate human skin and cause a burning sensation. They may possess a venom (Halstead 1956). Nevertheless, intestines of *C. imperialis* were often observed literally packed with these setae. The polychaete is typically found under rocks or in crevices in coral. Its food is unknown.

On several occasions, specimens of *Eurythoe complanata* were fed to *Conus imperialis* in the laboratory. The stinging operation is typical. Like *C. striatus*, *C. imperialis* uses its radula tooth as a harpoon. The tooth is not freed from the proboscis, but the impaled prey is drawn into the mouth by rapid contraction of the proboscis.

Only four prey organisms were recovered from the alimentary tracts of 20 specimens of *Conus pulicarius* which were examined. These were sufficient to show that the food of this species is not restricted to polychaetes. Two of the food organisms were of the species of capitellid eaten by *C. flavidus*, but the other two were of the echiuroid worm, *Thalassema* sp. Both of the latter were regurgitated by the snails after capture. At least one of the echiuroids was alive when regurgitated. This suggests that *Thalassema* may not be stung before being swallowed by *C. pulicarius*.

All of the other four vermivorous species of *Conus* collected on the reefs may be restricted to Eunicidae for food, although the samples examined were small. The primary food of *C. distans* is *Eunice afra*. This polychaete was found most commonly completely buried in coral rocks or in coral or other calcareous

encrustation on basalt boulders. *C. miles* feeds chiefly on *Lysidice collaris*, and *C. vexillum*, on *Eunice antennata* and *Marphysa sanguinea*. A single specimen of *E. afra* was recovered from the alimentary tract of *C. vitulinus*.

The large differences in the specific nature of the prey of the vermivorous species of *Conus* on reef platforms would seem to virtually preclude the possibility of interspecific competition for food. It was nevertheless of interest to obtain some information on the abundance of the prey species.

In order to determine the species and abundance of polychaetes associated with, or burrowing into, limestone, coral and coral ruble, sample blocks of substratum were removed from reefs and placed in sea water in sealed jars. When the oxygen tension decreased, the polychaetes were attracted out of their burrows and eventually fell to the bottom of the jar. After 2-3 days, the contents of the jar were fixed in 10% formalin. Cracking of pieces of coral revealed few or no polychaetes remaining within the blocks after this treatment. Dry weight, volume and surface (projection) area of the blocks were determined. Polychaetes equal to or greater than 0.3 mm in maximum diameter were identified and preserved.

The results of samples from Stations 3 and 7 treated in this manner are shown in Table 14. In suitable areas on reefs eunicids are seen to be extremely abundant. It is difficult, however, to assess the density of polychaetes over the entire reef platform, since the relative areas of different types of substratum could not be adequately measured. The data in Table 14 probably give the correct order of magnitude for areas with a predominantly lithified substratum.

MOLLUSCIVOROUS SPECIES

Two species of *Conus* found on subtidal reef platforms appear to feed exclusively on other gastropod mollusks. The species composition of their prey, as well as that of *C. textile*, found rarely on reefs, is shown in Table 15. In addition to specimens collected on reefs, total data include material collected in deeper water.

At least 13 species of prosobranchiate and opisthobranchiate gastropods were recorded from alimentary tract analyses of 146 specimens of *Conus pennaceus*. The most common food species is the bubble shell, *Haminoea crocata*. Second commonest is the small prosobranch, *Phasianella variabilis*. Since the shells of prosobranchs are not swallowed, the identification of partly digested remains was extremely difficult. About half of the prey organisms were identified to species, but this was not possible in some which were represented only by radulae and/or opercula.

Feeding of *Conus pennaceus* on *Haminoea crocata*, *Terebra gouldii* Deshayes, and *Cypraea maculifera* (Schilder) was observed in the laboratory. A specimen of *Cypraea moneta* Linné was not eaten, however, when left in a tank with two *C. pennaceus* for 24 hr. *C. pennaceus* did not prey on other species of *Conus*,

TABLE 14. Abundance of Polychaetes Associated with Hard Substrata on Reefs.

Sample No.	Station	Area (cm.²)	Species	Number Present
1269	7	50	Eunice (Niciaion) cariboea	6
			Cirriformia semicincta	2
			Eunice antennata	1
			Unidentified Polychaetes	6
				—
			Total	15
			Density of Large Polychaetes	3,000/m.²
			Density of Eunicidae	1,800/m.²
			(Number of Polychaetes <0.3 mm. diameter in sample	51)
1276	3	129	Eunice antennata	5
			Palola siciliensis	4
			Lysidice collaris	3
			Eunice (Nicidion) cariboea	2
			Cirriformia semicincta	1
			Eurythoe complanata	1
			Platynereis dumerilii	1
				—
			Total	17
			Density of Large Polychaetes	1,300/m.²
			Density of Eunicidae	1,100/m.²

although several were retained in the same aquaria for several months.

The most striking aspect of the food of *Conus marmoreus* is that it appears to consist entirely of other species of *Conus*. Remains of *Conus* species were found in alimentary tracts of five of the seven specimens of this rather rare species which were examined. On 31 March 1956, Mr. Charles Sueishi observed a specimen in the act of feeding on *Conus abbreviatus* near Station 11. Dissection revealed the remains of a second *C. abbreviatus* in the intestine. On 6 July 1956, the writer observed a specimen in the act of feeding on *C. lividus* at Station 9.

A specimen of *Conus textile* collected at Station 15 by Miss Valerie Lang contained the radula sheath, operculum, and other remains of a *Conus pennaceus* in its alimentary tract. Another specimen, which had just eaten a *Conus striatus*, was collected by Dr. C. M. Burgess near Makua, Oahu. One other gastropod, a *Morula ochrostoma* (Blainville), was identified from the alimentary tracts of *C. textile* examined. In the laboratory, specimens of *C. textile* were observed to sting and consume *C. abbreviatus*, *C. ebraeus*, *C. lividus*, *Cypraea caputserpentis*, *Cypraea moneta*, *Turbo intercostalis* Menke, *Thais aperta* Blainville, and *Drupa morum* Lamarck, but they did not sting *C. flavidus* or *Helcioniscus argentatus* Nuttall.

PISCIVOROUS SPECIES

Conus striatus occurs sparsely on Hawaiian reef platforms. Remains of fishes from the five specimens which were examined could not be identified. A goat-fish (*Parupeneus* sp.) is known to be eaten by *C. striatus* in Micronesia (unpublished data). The other known piscivorous species, *C. catus* and *C. obscurus*, were not collected by the writer on reef platforms, but

TABLE 15. Food of Molluscivorous Species of *Conus* on Reefs.

	C. pennaceus All Reefs	C. marmoreus All Reefs	C. marmoreus Total	C. textile All Reefs	C. textile Total
No. Specimens Examined...	146	3	7	2	10
Haminoea crocata Pease	24	—	—	—	—
Haminoea sp. cf. H. aperta Pease	2	—	—	—	—
Haminoea sp. 1057.	1	—	—	—	—
Phasianella variabilis Pease	12	—	—	—	—
Dolabrifera olivacea Pease	7	—	—	—	—
Gastropod sp. 1963	4	—	—	—	—
Gastropod sp. 1964....	4	—	—	—	—
Trochus intextus Kiener	3	—	—	—	—
Turbo intercostalis Menke	2	—	—	—	—
Pleurobranchus sp. 1064.	2	—	—	—	—
Gastropod sp. 988.	2	—	—	—	—
Natica marochiensis Gmelin.	1	—	—	—	—
Conus abbreviatus Reeve	—	1	3	—	—
Conus lividus Hwass in Bruguiere	—	1	2	—	—
Conus sp.	—	—	1	—	—
Conus pennaceus Born	—	—	—	1	1
Conus striatus Linne	—	—	—	—	1
Morula ochrostoma Blainville.	—	—	—	—	1
Unidentified Gastropods.	7	—	—	—	3
Total Gastropods.	71	2	6	1	6
Unidentified Food.	23	1	1	1	1

References consulted in the identification of the mollusks in this table were Edmondson (1946), Ostergaard (1955), Pease (1860), and Pilsbry (1917, 1920).

Ostergaard (1950) reported the former species from Station 3.

SUMMARY OF FOOD AND FEEDING IN THE SUBTIDAL REEF HABITAT

Modifications of radula teeth which can be correlated with increased frequency of feeding on tube-dwelling polychaetes are present in many of the vermivorous species of *Conus* characteristic of the subtidal reef platform habitat. A forward projecting cone on the base, which may aid in retaining the tooth in the proboscis while the prey is extracted from its tube, is present in the two dominant reef species, *C. flavidus* and *C. lividus*. The former preys almost exclusively on tube-dwelling Terebellidae. Polychaetes preyed on by *C. lividus* are chiefly terebellids, but the dominant food species is the enteropneust *Ptychodera flava*. In addition to the basal cone, both *C. flavidus* and *C. lividus* possess a backward projecting spur on the shaft of the radula tooth, about one-third of the length from the base. Peile (1939) suggested that this structure may serve to prevent the tooth from being forced back into the proboscis on the impact of the sting.

The chief differences in the radula teeth of *Conus lividus* and *C. flavidus* are that the latter is shorter and is finely serrate (in disagreement with Peile 1939), while the former has a long shaft and no serrations. There is no obvious adaptive significance to these differences; nevertheless, the difference in nature of the food of the two species is highly significant ($P < 10^{-6}$).

The characteristics of the radula teeth of *Conus*

sponsalis, C. abbreviatus, C. ebraeus, and *C. rattus* were discussed above. Differences in the feeding habits of these species on reef platforms are apparent from inspection of Table 13. The feeding habits of *C. abbreviatus* and *C. rattus* are most similar to each other, but even these differ highly significantly (P = 10^{-6}) in the samples examined.

Conus imperialis, C. miles, C. vexillum, and *C. vitulinus* all possess the forward projecting cone on the base of the radula teeth. All feed primarily on polychaetes which either burrow into coral (Eunicidae) or live under rocks or in crevices (*Eurythoe*). The presence of the cone is therefore correlated with the habit of feeding on burrowing polychaetes, and it may well serve the function of aiding in the extraction of the worm from its tube, as suggested by Peile (1939). Distinct differences in the nature of the food of all of these species is also apparent from Table 13, although the samples are rather small for rigorous statistical analysis.

Conus distans, which also feeds on burrowing eunicids, does not possess the basal cone on the radula tooth, but the terminal knob is extremely large and may have the same function. The food of *C. distans* is similar to that of *C. rattus,* but the differences between them are highly significant (P $< 10^{-3}$).

On reef platforms as on marine benches, the nature of the food of each vermivorous species of *Conus* differs significantly from that of all other species. Thus these species avoid competition for food among each other. In addition, they are completely ecologically isolated, with respect to food, from *C. pennaceus,* which feeds only on a large number of other gastropods. Two other molluscivorous species, *C. marmoreus* and *C. textile,* occur only very rarely on reef platforms. *C. striatus* is the only piscivorous species collected by the author on the reefs, although small numbers of *C. catus* also occur in this habitat.

AMOUNT OF FOOD EATEN

Thorson (1956) has recently called attention to the need for more information on the quantity of food consumed by predators in order to understand the dynamics of benthic communities. A few data on predatory benthic fishes show that the daily food consumption is equal to 3-5% of the weight of plaice (Dawes 1930, 1931). Smith (1950) calculated rates of 1.1-2.4% in benthic fishes of Block Island Sound. Among the gastropods, young, growing specimens of *Polinices duplicata* Say, feeding on *Gemma gemma* Totten, consumed about 7% of their own weight per day. The rate in older *Polinices* was about 5% (Turner 1951). Higher rates of 10-25% were calculated for other predatory gastropods by Thorson (1958).

In the data on *Conus* which follow, dry weight of the predator (excluding shell) is compared with dry weight of the prey. Dry weights of *Conus* were measured following heating at 100°C for 48-96 hr, or by estimation from "alcohol weight" using the con-

version given by Holme (1953). Dry weights of polychaetes were determined by the method of Holme.

Enough specimens of *Perinereis helleri* were available to establish the relationship between maxilla length and body weight. Thus the weight of the prey organisms could be determined even if only the maxillae were found in the alimentary tract of the predator. Using data obtained with this method as well as from direct weighing of intact polychaetes found in crops, the amount of food (17 *P. helleri*) consumed by 17 adult *Conus ebraeus* was calculated to average 0.0049 ± 0.0005 g. Dry weight of the predators was 0.43 ± 0.02 g. Since the daily feeding rate was estimated to be one polychaete per snail, the daily food consumption of *C. ebraeus* is equal to about 1% of its own body weight. Average quantitative food consumption of the four dominant species of *Conus* on marine benches, in per cent of body weight per day, was:

C. sponsalis	4.6%
C. abbreviatus	3.4%
C. chaldaeus	1.2%
C. ebraeus	1.2%

The two smaller species consume proportionately more food per day than the larger species. The rates are somewhat lower than those cited above for other predatory gastropods. The reason is probably that all of the other figures are for temperate species, many of which do not feed in winter. Since the time available for feeding is shorter, the feeding rate during the season is likely to be higher than in a tropical gastropod such as *Conus,* which feeds at a constant rate throughout the year.

PREDATION ON *CONUS*

The extent of predation on *Conus* is difficult to evaluate. In the course of collecting trips, freshly dead fragments of *C. catus, C. rattus, C. abbreviatus,* and *C. flavidus* were observed on marine benches. In some cases, shells had been broken into many pieces so recently that most of the pieces were present within a few square centimeters. On reef platforms, shell fragments of freshly killed specimens of 11 species of *Conus* were collected. Fragments of the relatively thin-shelled *C. pennaceus* were found most often. Surprisingly, fragments of the extremely thick-shelled *C. flavidus* were second commonest. These cases are believed due to predation. The identity of the predators is not known, but parrot fishes (Scaridae) and the zebra eel, *Echidna zebra* (Shaw) are possibly responsible.

Other organisms, including the other species of *Conus* mentioned in the previous section, other gastropods (*Cymatium*), and starfish (*Asterope*), were observed to prey on *Conus* in the laboratory.

Cymatium nicobaricum Röding readily attacked *Conus* in laboratory aquaria. A large specimen (shell length 84 mm) devoured specimens of *C. ebraeus, C. abbreviatus,* and *C. catus.* Dead *C. ebraeus* were also eaten. In one case, a live *Conus ebraeus* was attacked by *Cymatium nicobaricum* about 20 min after the two

were placed in the same aquarium. The predator introduced its proboscis into the aperture of the *Conus* shell, and apparently began to rasp off pieces of the foot with its radula. This position was maintained for 9 days, after which the empty *Conus* shell was released. *Cymatium*, which is represented by several species in Hawaii, is a likely predator of *Conus* in nature.

Although specimens of the starfish *Asterope carinifera* Lamarck were kept for months in aquaria with several species of *Conus*, predation was observed only rarely. It is not known whether *Asterope* preys on *Conus* in nature. The starfish is not very common, and its habitat is often not shared by *Conus*. Both *Asterope* and *C. ebraeus*, which the starfish ate in the aquarium, were however found at Station 13.

Xanthid crabs also attacked *Conus* in laboratory aquaria. The attacks usually resulted in the outer lip of the shell being broken off. Crabs were never observed to succeed in killing the gastropods, probably because the latter could retract farther into the shell, and the older portions of the shell were too thick for the crabs to break. However, laboratory observations were made only on two thick-shelled species, *C. lividus* and *C. flavidus*. Crabs may prey more successfully on some of the thinner-shelled species.

Two species of fishes, a wrasse, *Stethojulis axillaris* (Quoy and Gaimard) and a goby, *Chlamydes cotticeps* (Steindachner), were reported by Strasburg (1953) to feed on the eggs of *Conus* in Hawaii. The problem of predation on larvae remains unstudied. Large numbers of free-swimming veligers are undoubtedly consumed by carnivorous planktivores. Many newly settled larvae probably fall prey to brittle stars (*Ophiocoma* spp.) which abound on the reefs.

FOOD CHAINS AND TROPHIC STRUCTURE OF THE COMMUNITY

The polychaetes on which the dominant marine bench species of *Conus* feed are mainly herbivorous. At Station 5, *Perinereis helleri* was found to feed chiefly on the blue-green alga, *Lyngbya majuscula*. Alimentary tracts of specimens collected at night were often full of the filaments of this alga. Eunicids also feed on *Lyngbya* as well as on other algae .

Since predation on adult *Conus* may be assumed to be negligible, a short food chain of three steps is indicated. Since the numbers of species at the two higher trophic levels are large, increased efficiency associated with a restricted diet can be achieved without detracting from community stability (MacArthur 1955).

Data presented above for biomass of polychaetes and *Conus*, together with dry weights of algal samples collected about halfway across the bench at Station 5, were used to calculate the biomass pyramid for the algae-polychaete-*Conus* food chain shown in Fig. 28. The dominant alga in the sample was *Laurencia* sp. Since this does not appear to be eaten by the polychaetes under discussion, only *Lyngbya majus-*

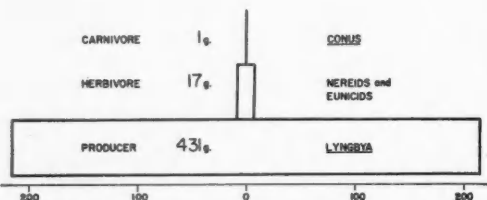*cula*, which represented 7% of the algae sample, is included in the pyramid.

Fig. 28. Pyramid of biomass for the algae-polychaete-*Conus* food chain at Station 5.

For this food chain, the ratios of standing crop between trophic levels are herbivores/producers 4% and carnivores/herbivores 6%. It is to be noted that these ratios apply only to the single food *chain* considered and not to the entire community or food *web*.

ECOLOGICAL NOTES ON OTHER SUBTIDAL HABITATS

The most important habitats of *Conus* in the Hawaiian Islands are the intertidal marine benches and subtidal reef platforms which have been discussed in the previous sections. The relatively fragmentary ecological information which has been gained concerning species which occur chiefly in other habitats is summarized in the following paragraphs.

Conus quercinus. Certain limited regions off the shore of Oahu, usually in bays, are characterized by vast areas of sand substratum uninterrupted by coral heads or limestone outcrops. Wave action is usually comparatively light, and the salinity is often somewhat reduced by the proximity of streams. Portions of such areas may be a foot or two above the 0 tide datum, forming a sand spit. Station 2A, Sand (Ahuolaka) Island, in Kaneohe Bay (Fig. 4), is such a formation. The habitat of *C. quercinus* appears to be restricted to areas of this type, at least at certain seasons. The writer's observations are in agreement with those of Bryan (1915), who stated "they (*C. quercinus*) appear to prefer the muddy brackish water conditions at the harbor mouth to a life on the coral reef in the open sea." The species is often common where it occurs, but its distribution in shallow water is probably limited by the sparse occurrence of favorable habitats about the Hawaiian Islands and by seasonal differences in habitat.

Collections made by the writer confirmed a marked seasonality of *Conus quercinus*, which had been verbally reported to him by a number of collectors. Collecting trips to Station 2A made by the writer between July, 1954, and June, 1956, are noted by closed circles in Fig. 29. A marked seasonal fluctuation in abundance, with maxima annually in February and March, is apparent. Since no quantitative sampling of the area was done, the absolute amplitude of the maxima is not meaningful.

The biological significance of the fluctuation in numbers of *Conus quercinus* is in reproduction.
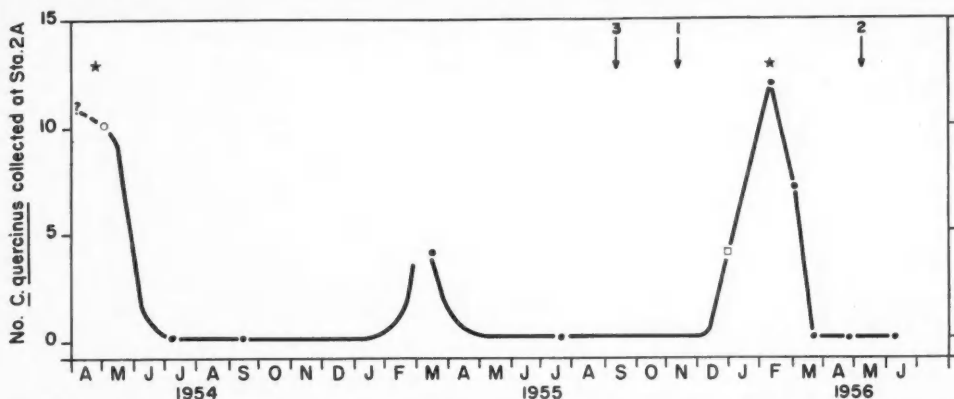
Fig. 29. Seasonal changes in abundance of *Conus quercinus* at Station 2A. Stars indicate observation of spawning of *C. quercinus* at Station 2A (1956) or in laboratory soon after being collected at Station 2A (1954). Closed circles indicate collecting trips by the author. Additional trips, during which no *C. quercinus* were seen, were made in August, 1954, and August, September, November, and December, 1955, but the exact dates were not recorded.

Explanation of vertical arrows: 1. Collection of one specimen in sampan channel, Kaneohe Bay, depth 10 ft, by A. H. Banner. 2. Collection of two specimens off Barbers Point, depth 160 ft, by R. Sheats. 3 Collection of two specimens in Bay ½ mile south of Hapuna Beach, Hawaii, depth 15-20 ft, by R. A. McKinsey.

Spawning was observed at Station 2A in February, 1956. A number of specimens collected at Station 2A in April, 1954, by staff members of the Hawaii Marine Laboratory, spawned in laboratory aquaria late the same month. The population apparently migrates to Station 2A from deeper water in early spring for spawning. The egg capsules are typically attached to the alga, *Acanthophora orientalis*. The adults then presumably return to deeper water. Specimens at Station 2A were collected in 2-10 ft of water and were most abundant in 2-5 ft. Other, "out of season" collection records from deeper water are also noted in Fig. 29.

Analysis of alimentary tract contents of 34 specimens of *Conus quercinus* revealed the commonest prey organism to be the enteropneust, *Ptychodera flava*, remains of which were found in 13 specimens. Two specimens contained remains of the sabellid polychaete, *Sabellastarte indica*. These were the only identifiable prey organisms. *Ptychodera flava* was extremely abundant at Station 2A; densities of several individuals per square foot were not uncommon.

Conus leopardus. The habitat of *Conus leopardus* is similar to that of *C. quercinus*, but the former species usually occurs in somewhat deeper water. It is rarely collected at depths of less than 10 ft. The deepest record known to the author is a specimen collected in 120 ft off Pearl Harbor, Oahu, by R. Sheats on 2 February 1956. Sand is the typical substratum, but specimens are also found on mixed sand-rubble bottoms.

No definitely identifiable food organisms were found in alimentary tracts of ten specimens which were examined. Remains in one specimen were tentatively identified as *Ptychodera flava*. The feeding of

C. leopardus on *P. flava* was observed in the laboratory. Within a few seconds after the enteropneust was introduced into an aquarium containing a *C. leopardus*, the latter became active, extending its siphon and waving it about in the water. Several minutes later, the orange rostrum extended and began to engulf the *Ptychodera*. At no time was the proboscis visible. The prey was apparently never stung, since rhythmic contractions of the proboscis, collar and trunk regions persisted until engulfment was complete, some 18 min later.

Conus leopardus is the largest species of the genus in Hawaiian waters, the shell lengths of some specimens exceeding 200 mm. However, its radula and venom apparatus are extremely poorly developed. The radula teeth of a 160-mm specimen measured only 0.9 mm in length, comparable to those of an adult (40-mm) *C. lividus*. It is just possible that the radula, which is an extremely specialized apparatus in other species of *Conus*, is vestigial in *C. leopardus*. It must be recalled however, that some species with well developed radula teeth do not always sting the prey prior to feeding.

Conus moreleti. No identifiable food organisms were found in alimentary tract contents of 6 specimens of *Conus moreleti* which were collected in depths of 10-40 ft off the leeward (west) coast of Oahu. However, this species, which is rather similar to *C. lividus*, is probably vermivorous.

Conus obscurus. Nine specimens collected at depths of 15-35 ft off leeward Oahu were examined. Remains of an unidentified fish were present in one. Attempts to observe the feeding process in the laboratory were not completely successful. Introduction of a fish into the vessel with the snail usually evoked

extension of the proboscis. In only one instance was
a radula tooth ejected, however. The fish, a specimen
of *Bathygobius fuscus,* escaped and was not swal-
lowed but died a few minutes later, presumably from
the effects of the venom.

Conus textile. Specimens were collected rarely
on the reefs and at depths of 10-75 ft. Results of
alimentary tract examinations are included in Table
15.

Conus miles. This species occurs occasionally on
reefs and benches but is somewhat more common in
deeper water. Individuals on reefs are usually larger,
however. Specimens collected in 35-40 ft off leeward
Oahu were found to have fed on *Lysidice collaris.*
(Most of the specimens of *C. moreleti, C. obscurus,
C. textile* and *C. miles* discussed in this section were
collected by R. M. Gray, R. A. McKinsey and C. M.
Stidham.)

DISCUSSION: ECOLOGICAL NICHES AND ECOLOGICAL ISOLATION

Odum (1953) satisfactorily defined ecological niche
as "the position or status of an organism within its
community and ecosystem resulting from the organ-
ism's structural adaptations, physiological responses,
and specific behavior." The ecological niche is multi-
dimensional.

In the preceding sections of this paper, the species
of *Conus* inhabiting Hawaiian coral reefs and marine
benches have been compared with respect to some of
the dimensions of niches. The purpose of this dis-
cussion is to state concisely all comparative data.
From these data, evidence of ecological isolation, or
its reciprocal, the overlap of ecological niches, will
be evaluated.

Formulation of the theory that ecological isola-
tion is the result of interspecific competition is due
to Volterra (1926; see also D'Ancona 1954). Since
Gause (1934) clearly showed that this theory was
applicable to experimental populations, the postulate
that in a stable community each species occupies a
different ecological niche and that two or more species
with the same ecological requirements cannot coexist
has become known as Gause's principle (Odum 1953),
Gause's hypothesis (Gilbert, Reynoldson & Hobart
1952), or, more properly, the Volterra-Gause prin-
ciple (Hutchinson 1953). In such experiments, only
one species finally survives in a population by inhibit-
ing the population(s) of the other species initially
present more than its own.

Although the process of competition can thus be
observed in experimental populations, it is very dif-
ficult to do so in natural populations. The reasons
for this are that (1) if the process occurs in nature,
its rate may be very slow, and (2) it is often difficult
to make the necessary determination of the behavior
of a species in the absence of its presumed competitor
in completely natural populations. It should be
pointed out that the demonstration of niches which
overlap with respect to one or more dimensions does
not prove the occurrence of competition. This seems

to have been overlooked by some authors (e.g. Test
1945, Odum 1953). In its most satisfactory defini-
tion, competition requires common exploitation of a
limited requisite. Furthermore, mechanisms by which
even species whose niches overlap with respect to
limited requisites can avoid severe competition have
been pointed out by Hutchinson (1953). Severe
competition is used here to mean competition leading
to the elimination of the less successful species.

Despite the inherent difficulties, interspecific com-
petition has been observed in nature, particularly in
birds, on a few occasions (Mackenzie 1950, Pitelka
1951, S. D. Ripley, verbal communication). The
rarity of such cases, together with the invocation of
other factors, led Andrewartha & Birch (1954) to a
general theory of population ecology without intro-
duction of the concept of competition. A number
of studies of natural populations containing eco-
logically similar species provide strong evidence of
a less direct sort in favor of the operation of inter-
specific competition in nature. Additional evidence
has been derived from studies of geographical re-
placement of species with "too slight ecological dis-
similarity" (Svärdson 1949a, 1949b).

In all carefully studied stable populations contain-
ing two or more ecologically similar species, more or
less subtle differences in the ecological niches of these
species have been elucidated, thus demonstrating the
validity of the Volterra-Gause principle in nature.
Ecologically *similar* species are just that and not
ecologically *identical.* It can be stated with Gilbert
et al. (1952), that these observations support the
hypothesis that "in a population of a species, mecha-
nisms which reduce competition between it and popu-
lations of other species tend to persist."

In the experimental studies of the Volterra-Gause
principle, avoidance of interspecific competition was
shown to be the result of such competition. In many
natural populations ecologically similar species co-
exist because of reduction or avoidance of competi-
tion. In this way, the evidence from natural popula-
tions favors the hypothesis that the process of compe-
tition, leading to the avoidance of competition, oper-
ates in nature, most probably as a selection pressure.

This evidence has been derived from studies of
natural populations which contain ecologically similar
species of many kinds, including flatworms (Beau-
champ & Ullyott 1932), fruit flies (Da Cunha, Dob-
zhansky & Sokoloff 1951), copepods (Hutchinson
1951), mollusks (Test 1945), fishes (Daiber 1956),
amphibians (Dumas 1956), birds (Lack 1945, 1947),
and mammals (McCabe & Blanchard 1951, Johnson
1943).

Except for a few papers which consider only one
dimension of the ecological niche, e.g. zonation (Fis-
cher-Piette 1935, Eslick 1940), the work of Test
(1945) is the only previous such study of marine
gastropods known to the writer. It deals with herbiv-
orous limpets, of the genus *Acmaea.* Test's work
differs from most of the others listed, and is more
similar to the present study, in that it deals with

TABLE 16. Summary of Ecological Characteristics of Species of *Conus* on Marine Benches.

	sponsalis	*abbreviatus*	*ebraeus*	*chaldaeus*	*rattus*	*catus*
Relative abundance at all bench stations............	1	2	3	4	5	6
Population density on a solution bench (Sta. 5) (no./100 sq. ft.)......................	0.41	0.66	1.02	0.15	0.02*	0.00
Population density on a water-leveled bench (Sta. Kl) (no./100 sq. ft.)......................	0.48	0.85	0.55	0.18	0.09	0.24
Population density at abrasion ramp stations* (no./100 sq. ft.)......................	0.25	0.21	0.00	0.07	0.33	0.00
Distance from shore of density peak at Sta. 5 (% distance across bench)...................	8%	8%	50%	73%	——	——
Distance from shore of density peak at Sta. Kl (% distance across bench)...................	22%	18%	26%	48-70%	47%	53%
Per cent of population on substratum of algal turf on bench, binding ± sand...................	90%	65%	65%	45%	62%	(45%)
Per cent of population on sand patches on bench.....	5%	26%	15%	28%	11%	(18%)
Per cent of population exposed to air at low tide.....	55%	35%	29%	32%	17%	29%
Per cent of population partly buried in substratum during day....................................	30%	63%	31%	42%	10%	(44%)
Ability to withstand strong water currents (exp't'l.) (arbitrary units)................................	+	+	++	+		
Active period in nature and in laboratory...........	All species actively crawl about at night, are quiescent during day					
Per cent of diet represented by Nereidae...........	52%	26%	93%	85%	50%	Eats Only Fish
Per cent of diet represented by Eunicea...........	44%	69%	6%	15%	50%	

*Calculated from time-relative density.

more than two ecologically similar sympatric species. As many as 17 species of *Acmaea* coexist in a broad region of the California coast. Test was able to show diversification of the ecological niches of these species, despite the demonstration of varying degrees of overlap in one or more dimensions of the niches. Only quite recently have similar studies been extended to large numbers of sympatric species in other groups, namely insects (Cooper & Dobzhansky 1956; Da Cunha, El-Tabey Shehata & de Olivera 1957) and birds (Betts 1955).

A total of 18 species of *Conus* were collected by the writer on Hawaiian coral reefs and marine benches. Of these, 16 were collected on reefs and 13 on benches, dispersed among these habitats as previously discussed. On marine benches, 6 of the 13 species present are characteristic of the habitat, and only these are included in the following discussion of ecological niches. Of the others, two represent unique collection records, and five are occasionally found on benches but are more typical of the reef habitat. The factors which probably limit their abundance on benches have been discussed above.

The ecology of the species of *Conus* inhabiting marine benches is complicated by the fact that the whole life cycle is not passed in the same habitat. Recruitment of all species is predominantly from pelagic veliger larvae which are washed onto benches from other areas of origin, particularly subtidal reefs, where conditions for spawning are more favorable.

The ecological requirements of pelagic larvae and newly metamorphosed young are unknown and are extremely difficult to study. Because of their small size, newly settled larvae are virtually impossible to observe in nature. Attempts to raise young from eggs in the laboratory generally failed. Veligers usually hatched and swam about freely but died before settling to the crawling mode of life. The food at these early stages is unknown. Veligers are probably plankton or seston feeders. It is not known whether or not newly settled larvae immediately assume the carnivorous habit, or at what stage the venom apparatus becomes functional.

Requisites which govern population density of pelagic veligers and newly-settled young stages may affect the observed adult population densities reported here. Predation may well be an important factor. These statements are, however, not based on positive evidence. The hypothesis was not amenable to investigation in the time available, so adult populations only were studied. The evidence to be summarized in Tables 16-20 suggests that adults of all species studied are sufficiently isolated ecologically that interspecific competition does not limit population densities.

In Table 16, all characteristics of ecological niches studied are summarized for the six most abundant species of *Conus* on marine benches. All of these species also occur in the subtidal reef habitat, although usually in considerably lower abundance. In Table 17, data for the 8 most abundant species on subtidal reefs are similarly summarized.

In order to determine the significance in niche differentiation of interspecific differences with respect to dimensions of niches, the results of statistical analyses of all observed ecological data relating to these species are summarized in Tables 18-20. In the right column of these tables the category of relationship of *Conus* to a number of environmental factors is listed. The statistical test applied to the data and the probability of the samples of the two species having been drawn at random from the same population are given in the second and third columns, respectively. Probabilities in most cases are extremely low. However, it is not legitimate to attribute all

TABLE 17. Summary of Ecological Characteristics of Species of *Conus* on Subtidal Reefs.

	flavidus	*lividus*	*pennaceus*	*abbreviatus*	*ebraeus*	*sponsalis*	*rattus*	*imperialis*
Relative abundance at all reef stations	1	2	3	4	5	6	7	8
Population density on a reef platform (Sta. K3) (no./100 sq. ft.)	0.03	—	—	0.07	0.09	—	—	—
Per cent of population on sand substratum	56%	64%	75%	78%	61%	38%	22%	48%
Per cent of population on reef limestone substratum	26%	22%	21%	13%	20%	30%	38%	26 %
Per cent of population on coral, rubble and rough coral bench substrata	18%	14%	4%	4%	19%	23%	40%	26%
Dominant component of particulate sediments		coarse+very coarse sand	coarse sand		coarse+very coarse sand			fine to coarse sand
Per cent of population buried or under rocks during day	15%	10%	100%	54%	27%	13%	14%	8%
Per cent of diet represented by Nereidae	—	—	—	—	15%	46%	23%	—
Per cent of diet represented by Eunicea	—	12%	—	100%	82%	50%	77%	27%
Per cent of diet represented by Terebellidae	64%	14%	—	—	—	—	—	—
Per cent of diet represented by all polychaetes	96%	39%	Eats only Gastropods	100%	100%	100%	100%	100%
Per cent of diet represented by enteropneusts	4%	61%	—	—	—	—	—	—

of the differences solely to the dimensions of the niches. If the degree of overlap is large, chi-square (but not Wilcoxon) tests may indicate significant differences if the sample also is large. A hypothetical case is illustrated in Fig. 30. In both both A and B, the probability that the two samples were drawn at random from the same population is the same. The ecological significance of the two situations is, however, quite distinct. Because of differences in position of the curves on the abscissa, competition between N_1 and N_2 for the requisite represented is much less likely in B than in A. Competition does not necessarily take place in either case.

For this reason the degree of overlap of the species with respect to each dimension is also included in Tables 18-20. In entries where the interspecific differences are highly significant, and where per cent overlap is large, the biological significance is less than the low probabilities might imply. That is, the possibility of competition is not virtually precluded.

Inspection of Table 16 shows as a first approximation that *Conus sponsalis* and *C. abbreviatus* are ecologically more similar to each other than to the other species in the table. These species are also similar in absolute abundance and in size. They are closely related systematically, usually being placed in the same subgenus (*Virroconus*). The results of statistical analyses of all observed ecological data relating to these two species are summarized in Table 18. Population densities are similar at the two most thoroughly studied bench stations, but they differ significantly when all marine benches are considered. The great difference in abundance on different reefs is due to the fact that *C. sponsalis* is much more abundant than *C. abbreviatus* at Station 7 and less abundant at all other

TABLE 18. Statistical Analyses of Ecological Data: Comparison of the Ecological Niches of *Conus sponsalis* and *C. abbreviatus*.

Relation of *Conus* to Environmental Factor	Statistical Test	P	Per cent Overlap
1. Relative abundance at Stations 5 and Kl	Chi-square	.8	95%
2. Relative abundance on three types of benches	Chi-square	<.01	53%
3. Relative abundance on four reefs	Chi-square	<10⁻⁶	14%
4. Distribution pattern on a solution bench (Sta. 5)	Wilcoxon	≫.05	80%
5. Distribution pattern on a water-leveled bench (Sta. Kl)	Wilcoxon	≫.05	80%
6. Occupation of different types of substratum on marine benches	Chi-square	<.001	62%
7. Occupation of different types of substratum on reefs	Chi-square	10⁻⁵	42%
8. Frequency of burrowing into substratum during day: marine benches	Chi-square	<.01	50%
9. Frequency of burrowing into substratum during day: reefs	Chi-square	≪.001	42%
10. Frequency of exposure to dry air at low tide on marine benches	Chi-square	<.01	67%
11. Nature of food: Frequency of Eunicea and Nereidae eaten on marine benches	Chi-square	<.001	59%
12. Nature of food: Frequency of individual prey species on benches	Chi-square	10⁻⁶	42%
13. Nature of food: Frequency of Eunicea and Nereidae eaten on reefs	Chi-square	≪.01	34%
14. Nature of food: Frequency of individual prey species on reefs	Chi-square	<10⁻⁶	25%
15. Food preference in choice experiments	Chi-square	<.001	48%

Entries 8, 10, and 11, are dependent on 7, 12, and 13, respectively.

reef stations. Both species are almost identically distributed over the benches where both are abundant. Despite the fact that both are common in the same habitat, the two species differ at the 1% level of significance with respect to all other dimensions of the
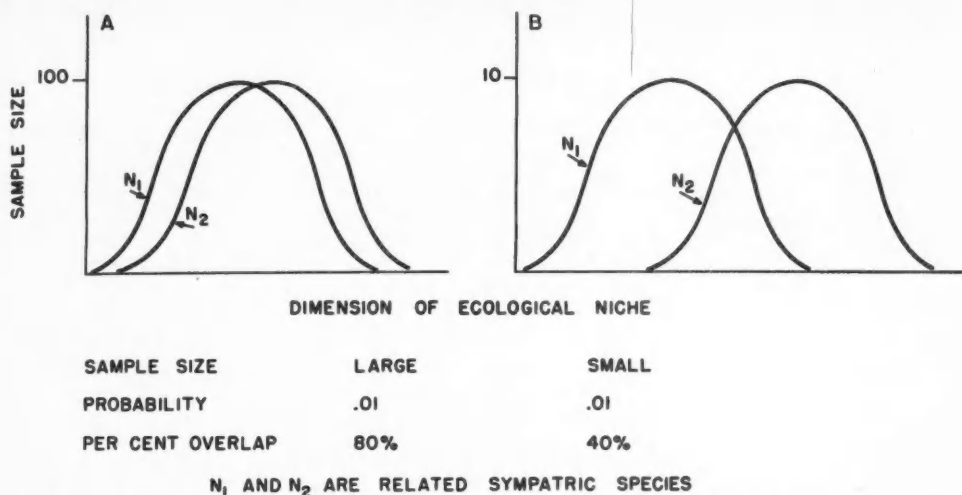
FIG. 30. Hypothetical case indicating the possibility of interspecific competition despite apparent statistically significant difference in niches. Explanation in text.

ecological niches which were investigated. Furthermore, the degree of overlap is small, hence ecological isolation is pronounced, with respect to all other factors.

Conus ebraeus and *C. chaldaeus* are the two species which are most closely related systematically. Both belong to the same subgenus (*Virroconus*) as *C. sponsalis* and *C. abbreviatus*. Many authors have considered *C. chaldaeus* to be a variety of *C. ebraeus*. This view has persisted among a few recent workers (e.g. Dodge 1953). Usually, however, both are accorded specific rank, and even opponents of this view have acknowledged the absence of intergrades. In Hawaii, the shells of these two species are quite distinct in appearance, much more so than in other parts of their range (Kohn unpublished.).

Furthermore, evidence discussed above and summarized in Table 19 indicates that the microhabitats of *Conus ebraeus* and *C. chaldaeus* are quite distinct, although the two species are typically found together in the marine bench macrohabitat. Since *C. ebraeus* is fairly common on reef platforms, but *C. chaldaeus* is virtually excluded, all of the comparisons in Table 19 are concerned only with marine benches. There the relative abundance, relation to substratum, frequency of exposure to air at low tide, and general nature of the food are very similar. However, striking differences in pattern of distribution across benches and especially in the specific nature of the food are apparent. The degree of overlap between the niches with respect to these two dimensions is extremely small. The two species are thus able to coexist and avoid interspecific competition.

Inspection of Tables 16 and 17 suggests that *Conus ebraeus* is ecologically about as similar to *C. abbreviatus* as it is to *C. sponsalis*. A similar comparison of the ecological data of *C. ebraeus* and *C. sponsalis* was also made. These two species differ

TABLE 19. Statistical Analyses of Ecological Data: Comparison of the Ecological Niches of *Conus ebraeus* and *C. chaldaeus* on Marine Benches.

Relation of *Conus* to Environmental Factor	Statistical Test	P	Per cent Overlap
1. Relative abundance at Stations 5 and Kl	Chi-square	.2	71%
2. Relative abundance on three types of benches	Chi-square	.03	80%
3. Distribution pattern on a solution bench (Sta. 5)	Wilcoxon	<.01	59%[†]
4. Distribution pattern on a water-leveled bench (Sta. Kl)	Wilcoxon	<.01	14%[*]
5. Occupation of different types of substratum	Chi-square	.17	63%
6. Frequency of burrowing into substratum during day	Chi-square	.6	80%
7. Frequency of exposure to dry air at low tide	Chi-square	.6	94%
8. Occupation of particulate sediments with different mechanical properties	Wilcoxon	.05	75%
9. Nature of food: Frequency of Nereidae and Eunicea eaten	Chi-square	.22	83%
10. Nature of food: Frequency of individual prey species	Chi-square	<10⁻⁶	0.5%

Entry 9 is dependent on entry 10.
†Overlap=3% if only 2nd and 3rd quartiles of the distribution shown in Figure 20 are considered.
*Overlap=0% if only 2nd and 3rd quartiles of the distribution shown in Figure 22 are considered.

significantly from each other with respect to almost all of the dimensions of ecological niches which were studied.

Inspection of Tables 16 and 17 suggests that *Conus rattus* is ecologically quite similar to *C. ebraeus*. *C. rattus* is placed in a different subgenus (*Lithoconus* or *Rhizoconus*) from the other bench species. An analysis similar to those of Tables 18 and 19 indicated that differences with respect to several dimensions of the niches of the two species are not significant and that there is considerable overlap. However, the two species are usually not found in the same

place, for *C. rattus* dominates the abrasion ramp benches where *C. ebraeus* is absent. Where both occur, *C. ebraeus* is the more successful, judging from absolute numbers of both present on solution benches, water-leveled benches, and reef platforms. The difference between the food of these two species is also highly significant. On marine benches, the food of *C. rattus* is most similar to that of *C. sponsalis* (P = .7 in comparison of families of polychaetes eaten), but the individual species preyed on by *C. rattus* and *C. sponsalis* differ highly significantly (P $< 10^{-6}$), and the overlap is only 22%.

Of the species of *Conus* characteristic of marine benches, *C. catus* (subgenus *Chelyconus*) was the least abundant. This species was commonest at Station K1, where its greatest density was nearer the outer edge than any other species present (Fig. 22). Samples were too small to provide reliable information on most other characteristics of the niche. However, *C. catus* is completely ecologically isolated from all other species of *Conus* which inhabit marine benches by the nature of its food, which consists entirely of fishes.

Turning to the species characteristic of subtidal reef platforms, it is apparent from Table 17 that *Conus flavidus* and *C. lividus,* the two most abundant species, are very similar ecologically. Since both occur uncommonly on marine benches, only data from reef stations are presented in Table 20, which summarizes the comparative ecology of these two species.

TABLE 20. Statistical Analyses of Ecological Data: Comparison of the Ecological Niches of *Conus lividus* and *C. flavidus* on reefs.

Relation of *Conus* to Environmental Factor	Statistical Test	P	Per cent Overlap
1. Relative abundance on four reefs (Stations 3, 4, 7, 9)	Chi-square	.001	64%
2. Relative abundance on three reefs (Stations 3, 4, 9)	Chi-square	.08	75%
3. Distribution pattern on three reefs.....	Wilcoxon	$\gg$.05	88%
4. Occupation of different types of substratum......................	Chi-square	.15	77%
5. Association with particulate sediments with different mechanical properties.	Wilcoxon	.05	42%
6. Nature of food: Frequency of major groups eaten*	Chi-square	$<10^{-6}$	12%
7. Nature of food: Frequency of individual prey species eaten.................	Chi-square	$<10^{-6}$	10%

*Major groups=Terebellidae, other polychaetes, and enteropneusts

On most reefs, the abundance of *C. flavidus* and *C. lividus* is similar. An exception is Station 7, where the latter species was much the more abundant. The significant difference in abundance in the first entry of Table 20 is due entirely to Station 7, as the second entry shows. The nature of, and relation to, the substratum is similar in both species. The most striking difference in the ecological niches of *C. flavidus* and *C. lividus* is in the nature of the food. Frequency differences in the samples examined are highly significant, and degree of overlap is exceedingly low. There is thus little possibility of competition for food.

Extensive overlapping with respect to other environmental requisites may permit competition, however.

A number of vermivorous species occur on reefs in very low population densities. Three of these, *Conus distans, C. vexillum* and *C. imperialis,* attain a larger size than almost all of the other species found on the reefs. Specimens of *C. distans* collected ranged from 46 to 131 mm in shell length; the range in *C. vexillum* was 44-85 mm, and in *C. imperialis,* 52-88 mm. These species, as well as *C. miles* and *C. vitulinus,* feed on eunicid polychaetes. Some of these species may be restricted to eunicids for food, but *C. imperialis* also feeds on the amphinomid polychaete, *Eurythoe complanata.* Since the samples collected were small, little statistical information was obtained. However, the data presented in Table 13 suggest striking differences in the specific nature of the prey of these species and, therefore, in that dimension of their ecological niches. The factors influencing population density are not known.

Two salient features of the niche of *Conus pulicarius* serve to isolate this species ecologically from its sympatric congeners. *C. pulicarius* occurs most often in large areas of deep sand on reef platforms, while the more abundant *C. flavidus* and *C. lividus* occur most often on patches of thin sand on reef limestone, or in small sandpockets. Secondly, part of the diet of *C. pulicarius* consists of the echiuroid, *Thalassema,* which as far as is known is not exploited for food by any other species of *Conus.* Information on the ecology of *Thalassema* is not sufficient to determine whether these two aspects of the niche of *C. pulicarius* are related.

The ecological niche of *Conus pennaceus* differs qualitatively from those of the other reef species with respect to both space and food. This species typically remains under basalt or coral rocks on, or partly buried in, sand during the day. Other species are found only rarely in this microhabitat. Competition for food with the numerous vermivorous species is completely avoided, since *C. pennaceus* feeds solely on other gastropods. The two other molluscivorous species, *C. marmoreus* and *C. textile,* are exceedingly rare on the reefs. Data obtained by the author are too few to indicate the extent of overlap with respect to food. However, both *C. marmoreus* and *C. textile* feed at least partly on other species of *Conus* while *C. pennaceus* was never found to eat its congeners.

The wide variety of gastropods on which *C. pennaceus* feeds is further evidence that intraspecific competition is of much greater importance than interspecific competition to this species. For, as Svärdson (1949a) showed, dominant intraspecific pressure causes a species to approach more closely the tolerance limits of its niche. "In this case, the species may be said to go down the slopes of its adaptive peak" (Svärdson 1949a).

Both piscivorous species, *Conus striatus* and *C. catus,* are very rare on Hawaiian reefs. They are ecologically isolated from all of the other species by the nature of their food. Young *C. striatus* may feed

on fishes of similar size to those eaten by adult *C. catus*, but the food of adult *C. striatus* is much larger.

The data presented in the preceding paragraphs indicate a high degree of ecological isolation among the species of *Conus* considered. Except where otherwise noted, each marine bench and subtidal reef habitat is a homogeneous one, containing a single community of *Conus*, as evidenced by agreement with the theoretical distribution given by MacArthur (1957). Although such agreement implies non-overlapping niches, this ideal is not completely realized in nature. As MacArthur (1957) showed, however, the distribution expected if niches overlapped randomly would fit the observed data much more poorly.

Ecological isolation results from fractionation of the habitat into microhabitats which differ especially with respect to zone occupied, relation to the substratum, and, especially, nature of the food. The first factor is of much greater importance on marine benches than on reef platforms. In this manner, interspecific competition severe enough to lead to the elimination of some of the species from the habitat is avoided. Such avoidance of competition is a likely result of the process of competition itself (Park 1954). But, as has been noted, direct evidence bearing on this is difficult to obtain from observation of natural populations (see also Mayr 1948).

Pertinent evidence obtained in the present study is that mentioned in connection with *Conus sponsalis*, which sometimes occurs where the ecologically similar *C. abbreviatus* is absent. Here the microhabitat is broadened to include, for example, more extensive use of eunicids for food. Also, *C. rattus* occurs in very low densities where *C. ebraeus* is abundant, but the former is the dominant species on the abrasion ramp type of marine bench, where the latter is absent. Restriction of the vermivorous species to apparently optimal regions of their possible habitats may also indicate the efficacy of interspecific competition, in accord with Svärdson (1949a).

In summary, density-inactive factors of the environment (Nicholson 1955) permit certain species of *Conus* to occur in the marine bench and subtidal reef habitats. Hydrographic characteristics and certain properties of the substratum are likely to be important factors of this type. The number of ecologically closely related species which may occupy a habitat is proportional to the amount of fractionation into microhabitats, which may overlap but are sufficiently distinct that severe interspecific competition is precluded. The process by which these microhabitats are established may be interspecific competition.

The population density is adjusted to certain governing requisites in the environment. Some of the species of *Conus* which occur on marine benches in Hawaii are believed to be limited by the extent of sand substrata suitable for burrowing (*C. pennaceus*) or required by prey organisms (*C. lividus*, *C. flavidus*). Six other species on marine benches may be termed dominants in this habitat. Of these, the population size of *C. catus* may be limited by the

amount of available food. Population densities of the more abundant species on reefs may also be limited by the amount of available food. Governing requisites of the other species are probably not amount of adult food, space, or predators. Factors which are effective at a pre-adult stage in the life history, which were not amenable to study, are likely to be important.

SUMMARY

The gastropod genus *Conus* has contributed to the enrichment of the number of species of epifaunal marine invertebrates in tropical regions in that it is typically represented by many sympatric species. Ecological observations on 25 species which occur in the Hawaiian Islands are reported. Most of the data concern natural populations of 18 species studied on intertidal marine benches and subtidal coral reefs which fringe much of the coastline of the Islands. Investigations on marine benches were carried out at nine stations on the islands of Oahu, Kauai, and Maui. Eight subtidal reefs on Oahu and Kauai were studied.

Conus populations on marine benches are composed chiefly of adult individuals. A stable population density of about 2.5 individuals/100 sq ft (30/100m^2) may be expected on solution benches and water-leveled benches. Mean density of a few quantitative samples on a reef was 0.16 individual/100 sq ft (2/100m^2). Although populations are much denser on marine benches, spawning is usually unsuccessful there, presumably because of the absence of protected sites for the attachment of egg capsules. Recruitment is from pelagic veliger larvae which originate elsewhere but are carried to benches in condition to settle and assume the benthic mode of life.

Four species (*Conus sponsalis*, *C. abbreviatus*, *C. ebraeus*, and *C. chaldaeus*) are usually dominant on solution benches and water-leveled benches. *C. rattus* is the most abundant species on abrasion ramp benches. *C. catus* is also a typical inhabitant of marine benches. *C. distans*, *C. flavidus*, *C. lividus*, *C. miles*, *C. pennaceus*, *C. nussatella*, *C. retifer*, and juvenile *C. vexillum* were also recorded from marine benches.

Conus flavidus and *C. lividus* are the dominant species on subtidal reefs, although at one station *C. sponsalis* was most abundant. *C. pennaceus*, *C. abbreviatus*, *C. ebraeus*, and *C. rattus* are also common. Other species recorded from reef stations were *C. imperialis*, *C. distans*, *C. chaldaeus*, *C. marmoreus*, *C. miles*, *C. pulicarius*, *C. striatus*, *C. textile*, *C. vexillum*, and *C. vitulinus*.

Values of an index of diversity, which measured similarity of species composition of different populations, differed but little in comparisons a) among the several bench stations, b) among the several reef stations, and c) between reef and bench stations. Quantitatively, however, certain species are characteristically most abundant on benches, while others are most abundant on reefs. Calculation of a measure of heterogeneity gave low values when the *Conus* com-

munities of reefs were compared among each other ($H' = .09$) and when the communities of benches were compared among each other ($H' = .19$). Comparison of summed reef populations with summed bench populations showed much greater heterogeneity ($H' = .84$).

At the most thoroughly studied bench and reef stations, number of species and number of individuals are related in a manner which agrees with the theoretical distribution expected in an adequately sampled, homogeneous community of a single habitat, where niches are non-overlapping and continuous.

Fractionation of the habitat into microhabitats was observed but, as expected intuitively, it is not complete. On marine benches, the species present are non-randomly distributed across the bench platform from shore to seaward edge. The distributions of *Conus sponsalis* and *C. abbreviatus* are similar. Those of all other species differ significantly from each other at the 5% level of probability. The number and biomass of *Conus* decreases from a maximum near the landward edge to the seaward edge.

On reef platforms, the distribution of *Conus* is characterized by patchiness, or clumping, which is correlated with the nature of the substratum. Distribution is not related to distance from shore or breaker line, except that density is low at both extremes. Over most of the reef platform, the observed distribution reflects the uniformity of water movements across the reef.

Differential association with different kinds of substratum on marine benches serves to partially distinguish the microhabitats of *Conus sponsalis* and *C. abbreviatus*, the latter occurring more often in sandier regions. This is correlated with the observation that *C. abbreviatus* burrows in the substratum significantly more often than *C. sponsalis*. Although these two species commonly coexist, only *C. sponsalis* was found on benches or parts of benches exposed to dry air for long periods at low tide.

On Hawaiian coral reefs, most species of *Conus* are most often found associated with sand, the most prevalent type of substratum. Only one species, *C. pulicarius*, is probably entirely restricted to a sand substratum. The two most abundant species on the reefs, *C. flavidus* and *C. lividus*, occur characteristically on patches of sand among solid substratum. *C. abbreviatus*, which occupies sandier regions of marine benches, is also a sand dweller on the reefs. *C. pennaceus* characteristically occurs on or partly buried in sand under basalt or coral rocks during the day but crawls about on the surface of the sand at night. Other species are not commonly found under rocks.

Mechanical analyses of sand suggested no niche diversification with respect to particle size distribution of this moiety of the substratum.

Alimentary tracts of 1,930 specimens of 24 species of *Conus* collected in Hawaii were examined. From these, 1,073 prey organisms were identified, 879 of them to species. Three groups of species within the genus *Conus* may be distinguished on the basis of the nature of the food: most species feed exclusively on worms, mainly polychaetes. A second group feeds exclusively on other gastropods, and the third group feeds only on fishes. Eleven species, *C. sponsalis*, *C. abbreviatus*, *C. ebraeus*, *C. chaldaeus*, *C. rattus*, *C. distans*, *C. miles*, *C. imperialis*, *C. vexillum*, *C. vitulinus*, and *C. pertusus*, feed exclusively on polychaetes. Samples of the last three named species were rather small, however. Three species, *C. lividus*, *C. flavidus* and *C. quercinus*, feed both on polychaetes and on the enteropneust, *Ptychodera*. *C. leopardus* probably feeds on *Ptychodera*. *C. pulicarius* eats polychaetes and the echiuroid, *Thalassema*. *C. pennaceus*, *C. marmoreus*, and *C. textile* feed exclusively on other gastropods. *C. striatus*, *C. catus* and *C. obscurus* feed only on fishes.

On marine benches, the vermivorous species of *Conus* prey almost exclusively on members of the polychaete family Nereidae and superfamily Eunicea. At one station, the species *Perinereis helleri* was found to be the primary food of the three most abundant species of *Conus*. This polychaete was so abundant, however, that food cannot be said to be in short supply. Interspecific competition for food is therefore not indicated. Species of *Conus* common to both habitats feed proportionately more often on eunicids on reef platforms than they do on marine benches, for nereids are uncommon in the former habitat.

The typically reef-dwelling vermivorous species feed chiefly on polychaetes and enteropneusts associated with the sand moiety of the substratum. Of the two dominant species, *Conus flavidus* eats mainly Terebellidae, and *C. lividus* eats mainly *Ptychodera*.

On marine benches, the dominant species of *Conus* eat polychaetes which feed on algae, forming a three-step food chain. Calculation of a biomass pyramid for this food chain gave an herbivore/producer ratio of 4% and a carnivore/herbivore ratio of 6%.

Predation on *Conus* was difficult to measure. Certain fishes, other gastropods, octopi, crabs and starfishes are possible predators on adults. Predation on free-swimming larvae and newly-settled young is presumably of major ecological significance, but it was not amenable to investigation. Other factors which may also govern population density of the various species are also considered.

Ecological niches, ecological isolation, and interspecific competition in natural populations are discussed briefly. The comparative ecology of the more abundant species of *Conus* is summarized in the discussion, with emphasis on the extent of ecological isolation. Statistical analyses of certain dimensions of the niches of the ecologically most similar species are presented. Limitations of simple tests of significance of differences are noted. Degree of overlap is extremely important in niche diversification.

The adult ecological niche of each species of *Conus* studied differs significantly with respect to at least two of the following characteristics: nature of the food, nature of and relation to the substratum, and

zonation or distribution pattern. The last is of particular importance only on marine benches. These differences are concluded to be the primary factors by which the ecological niches of species of *Conus* are differentiated. This is the mechanism which enables the maintenance of populations of large numbers of closely related, sympatric species of *Conus* in tropical regions.

LITERATURE CITED

Abbott, D. P. 1946. Some polychaetous annelids from a Hawaiian fish pond. Univ. Hawaii Res. Publ. No. 23: 5-24.

Alpers, F. 1931. Zur kenntnis der anatomie von *Conus lividus* Brug., besonders des darmkanals. Jena. Zeitschr. Naturwiss. **65**: 587-658.

——. 1932a. Zur biologie des *Conus mediterraneus* Brug. Jena. Zeitschr. Naturwiss. **67**: 346-363.

——. 1932b. Ueber die nahrungsaufnahme von *Conus mediterraneus* Brug. eines toxoglossen prosobranchier. Pubbl. Staz. Zool. Napoli **11**: 426-445.

Andrewartha, H. G. & L. C. Birch. 1954. The Distribution and Abundance of Animals. Chicago: University of Chicago. 782 pp.

Banner, A. H. 1953. The Crangonidae, or snapping shrimp, of Hawaii. Pac. Sci. **7**: 3-144.

Beauchamp, R. S. A. & P. Ullyott. 1932. Competitive relationships between certain species of fresh-water triclads. Jour. Ecol. **20**: 200-208.

Bergh, R. 1896. Beiträge zur kenntnis der coniden. Nova Acta Ksl. Leop.-Carol. Akad. Naturf. **65**: 67-214.

Betts, M. M. 1955. The food of titmice in oak woodland. Jour. Anim. Ecol. **24**: 282-323.

Brown, F. A. Jr., M. Fingerman, M. I. Sandeen & H. M. Webb. 1953. Persistent diurnal and tidal rhythms of color change in the fiddler crab, *Uca pugnax*. Jour. Exp. Zool. **123**: 29-60.

Bryan, W. A. 1915. Natural History of Hawaii. Honolulu: Hawaiian Gazette Co. 596 pp.

Clements, F. E. & V. E. Shelford. 1939. Bio-Ecology. New York: John Wiley & Sons. 425 pp.

Clench, W. J. & Y. Kondo. 1943. The poison cone shell. Amer. Jour. Trop. Med. & Hyg. **23**: 105-121.

Cooper, D. M. & T. Dobzhansky. 1956. Studies on the ecology of *Drosophila* in the Yosemite region of California. I. The occurrence of species of *Drosophila* in different life zones and at different seasons. Ecology **37**: 526-533.

Crombie, A. C. 1947. Interspecific competition. Jour. Anim. Ecol. **16**: 44-73.

Da Cunha, A. B., T. Dobzhansky & A. Sokoloff. 1951. On food preferences of sympatric species of *Drosophila*. Evolution **5**: 97-101.:

Da Cunha, A. B., A. M. El-Tabey Shehata & W. de Oliveira. 1957. A study of the diet and nutritional preferences of tropical species of *Drosophila*. Ecology **38**: 98-106.

Daiber, F. C. 1956. A comparative analysis of the winter feeding habits of two benthic stream fishes. Copeia **1956**: 141-151.

D'Ancona, U. 1954. The struggle for existence. Leiden: W. J. Brill. 274 pp.

Darwin, C. 1859. On the origin of species by means of natural selection. London: J. Murray. 502 pp.

Dawes, B. 1930. Growth and maintenance in the plaice (*Pleuronectes platessa* L.). Part I. Jour. Mar. Biol. Assn. U. K. **17**: 103-147.

——. 1931. Growth and maintenance in the plaice (*P. platessa* L.) Part II. Jour. Mar. Biol. Assn. U. K. **17**: 877-947.

Dodge, H. 1953. A historical review of the mollusks of Linnaeus. Part 2. The class Cephalopoda and the genera *Conus* and *Cypraea* of the class Gastropoda. Bull. Amer. Mus. Nat. Hist. **103**: 1-134.

Dumas, P. C. 1956. The ecological relations of sympatry in *Plethodon dunni* and *Plethodon vehiculum*. Ecology **37**: 484-495.

Edmondson, C. H. 1928. The ecology of an Hawaiian coral reef. B. P. Bishop Mus. Bull. **45**. 64 pp.

——. 1946. Reef and shore fauna of Hawaii. B. P. Bishop Mus. Spec. Pub. **22**, 381 pp.

Eslick, A. 1940. An ecological study of *Patella* at Port St. Mary, Isle of Man. Proc. Linn. Soc. Lond. **152**: 45-59.

Fauvel, P. 1927. Polychètes Sédentaires. Faune de France, **16**. 494 pp.

Fischer-Piette, E. 1935. Les patelles d'Europe et d'Afrique du nord. Jour. Conchyl. **79**: 5-66.

Gause, G. F. 1934. The Struggle for Existence. Baltimore: Williams and Wilkins. 163 pp.

Gilbert, O., J. B. Reynoldson & J. Hobart. 1952. Gause's hypothesis: an examination. Jour. Anim. Ecol. **21**: 310-312.

Halstead, B. W. 1956. Animal phyla known to contain poisonous marine animals. Venoms (Amer. Assn. Adv. Sci.): 9-27.

Hartman, O. 1940. Polychaetous annelids. II. Chrysopetalidae to Goniadidae. Allan Hancock Pacific Expeditions **7**: 173-287.

——. 1944. Polychaetous annelids. V. Eunicea. Allan Hancock Pacific Expeditions **10**: 1-236.

——. 1948. The marine annelids erected by Kinberg, with notes on some other types in the Swedish State Museum. Ark. Zool. **42A**: 1-137.

——. 1954. Marine annelids from the northern Marshall Islands. Geol. Surv. Prof. Pap. **260-Q**: 619-644.

Helfrich, P. & A. J. Kohn. 1955. A survey to estimate the major biological effects of a dredging operation by the Lihue Plantation Co., Ltd. on North Kapaa Reef, Kapaa, Kauai. Preliminary Report. 31 pp. (Mimeographed. Available from the authors).

Hinegardner, R. T. 1957. The anatomy and histology of the venom apparatus in several gastropods of the genus *Conus*. M.S. Thesis, University of Southern California.

——. 1958. The venom apparatus of the cone shell. Hawaii Med. Jour. **17**: 533-536.

Holly, M. 1935. Polychaeta from Hawaii. B. P. Bishop Mus. Bull. **129**: 33 pp.

Holme, N. A. 1953. The biomass of the bottom fauna in the English Channel off Plymouth. Jour. Mar. Biol. Assn. U.K. **32**: 1-49.

——. 1954. The ecology of British species of *Ensis*. Jour. Mar. Biol. Assn. U.K. **33**: 145-172.

Hutchinson, G. E. 1951. Copepodology for the ornithologist. Ecology **32**: 571-577.

——. 1953. The concept of pattern in ecology. Proc. Acad. Nat. Sci. Phil. **105**: 1-12.

Johnson, D. E. 1943. Systematic review of the chipmunks (genus *Eutamias*) of California. Univ. Calif. Pub. Zool. **48**: 63-148.

Koch, L. F. 1957. Index of biotal dispersity. Ecology 38: 145-148.

Kohn, A. J. 1955. Studies on food and feeding of the cone shells, genus *Conus*. Ann. Rept. Amer. Malacol. Union, Bull. 22: 31.

———. 1956a. The ecology collecting sack modified for marine organisms. Turtox News 34: 33.

———. 1956b. Piscivorous gastropods of the genus *Conus*. Proc. Nat. Acad. Sci. 42: 168-171.

———. 1959. The Hawaiian species of *Conus*. Pac. Sci. (In Press).

Kohn, A. J. & P. Helfrich. 1957. Primary organic productivity of a Hawaiian coral reef. Limnol. & Oceanogr. 2: 241-251.

Lack, D. 1945. The ecology of closely related species with special reference to the cormorant (*Phalacrocorax carbo*) and shag (*P. aristotelis*). Jour. Anim. Ecol. 14: 12-16.

———. 1947. Darwin's Finches. Cambridge: University Press. 208 pp.

MacArthur, R. 1955. Fluctuations of animal populations, and a measure of community stability. Ecology 36: 533-536.

———. 1957. On the relative abundance of bird species. Proc. Nat. Acad. Sci. 43: 293-295.

Margalef, R. 1956. Información y diversidad específica en las communidades de organismos. Inv. Pesq. Barcelona 3: 99-106.

Mackenzie, J. M. D. 1950. Competition for nest-sites among hole-breeding species. Brit. Birds 43: 184-185.

Mayr, E. 1948. The bearing of the new systematics on general problems: The nature of species. Adv. Gen. 2: 205-237.

McCabe, T. T. & B. D. Blanchard. 1951. Three species of *Peromyscus*. Santa Barbara: Rood Associates. 136 pp.

McCaughey, V. 1918. A survey of the Hawaiian coral reefs. Amer. Nat. 52: 409-438.

Nicholson, A. J. 1955. An outline of the dynamics of animal populations. Austral. Jour. Zool. 2: 9-65.

Odum, E. P. 1953. Fundamentals of Ecology. Philadelphia: W. B. Saunders Co. 384 pp.

Odum, H. T. & E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25: 291-320.

Ohba, S. 1952. Analysis of activity rhythm in the marine gastropod, *Nassarius festivus*, inhabiting the tide pool. I. On the effect of tide and food in the daytime rhythm of activity. Annot. Zool. Japon. 25: 289-297.

Okuda, S. 1937. Polychaetous annelids from the Palau Islands and adjacent waters, the South Sea Islands. Bull. Biogeogr. Soc: Japan 7: 257-316.

Ostergaard, J. M. 1950. Spawning and development of some Hawaiian marine gastropods. Pac. Sci. 4: 75-115.

———. 1955. Some opisthobranchiate Mollusca from Hawaii. Pac. Sci. 9: 110-136.

Park, T. 1954. Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of *Tribolium*. Physiol. Zool. 27: 177-238.

Pease, W. H. 1860. Descriptions of new species of Mollusca from the Sandwich Islands. Proc. Zool. Soc. Lond. Pt. 27. 1860: 18-36.

Peile, A. J. 1939. Radula Notes VIII. 34. *Conus*. Proc. Malacol. Soc. Lond. 23: 348-355.

Pilsbry, H. A. 1917. Marine Mollusks of Hawaii, I-III. Proc. Acad. Nat. Sci. Phil. 69: 207-230.

———. 1920. Marine mollusks of Hawaii, XIV-XV. Proc. Acad. Nat. Sci. Phil. 72: 360-382.

Pitelka, F. A. 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen humming birds. Ecology 32: 641-661.

Prosser, C. L. 1955. Physiological variation in animals. Biol. Rev. 30: 229-262.

Sandeen, M. I., G. C. Stephens & F. A. Brown, Jr. 1954. Persistent daily and tidal rhythms of oxygen consumption in two species of marine snails. Physiol. Zool. 27: 350-356.

Smith, F. E. 1950. The benthos of Block Island Sound. Ph.D. Thesis, Yale University.

Strasburg, D. W. 1953. Comparative ecology of two salariin blennies. Ph.D. Thesis, University of Hawaii.

Svärdson, G. 1949a. Competition and habitat selection in birds. Oikos 1: 157-174.

———. 1949b. Competition between trout and char (*Salmo trutta* and *S. alpinus*). Report, Inst. Freshw. Res., Drottninghom 29: 108-111.

Takahashi, K. 1939. Polychaeta on coral reefs in Palau. Kagaku Nanyo (Science of the South Sea) 2: 18-29. (in Japanese)

Test, A. R. 1945. Ecology of California Acmaea. Ecology 26: 395-405.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. Medd. Komm. Havundersøg., Kbh., Plankton 4: 523 pp.

———. 1956. Marine level-bottom communities of recent seas, their temperature adaptation and their "balance" between predators and food animals. Trans. N.Y. Acad. Sci. 18: 693-700.

———. 1958. Parallel level bottom communities, their temperature adaptation and their "balance" between predators and food animals. *In* Perspectives in Marine Biology. Berkeley: University of California Press. 67-86.

Treadwell, A. L. 1906. Polychaetous annelids of the Hawaiian Islands collected by the steamer "Albatross" in 1902. U. S. Fish. Comm. Bull. 1903: 1145-1181.

———. 1922. Leodicidae from Fiji and Samoa. Carnegie Inst. Wash. Pub. No. 312: 127-170.

Turner, H. J. 1951. Fourth report on investigations of the shellfisheries of Massachusetts. State of Massachusetts. 21 pp.

Van Dongen, A. 1956. The preference of *Littorina obtusata* for Fucaceae. Arch. Néerl. Zool. 11: 373-386.

Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. Accad. Lincei. Ser. 6. 2: 31-113.

Wentworth, C. K. 1938. Marine bench-forming processes: Water-level benching. Jour. Geomorphol. 1: 6-32.

———. 1939. Marine bench-forming processes. II, solution benching. Jour. Geomorphol. 2: 3-25.

Wilson, D. P. 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* Savigny. Ann. Inst. Oceanogr. Monaco 27: 49-156.

———. 1955. The role of micro-organisms in the settlement of *Ophelia bicornis* Savigny. Jour. Mar. Biol. Assn. U.K. 34: 531-544.